

STUDIES ON THE VISUAL SYSTEM OF THE RABBIT

by

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"I am not eager to rehearse
My thought and theory....."

T.S.ELIOT, "Little Gidding".

PREFACE

Because the work in this thesis covers a wide variety of topics it was decided to diverge from the traditional arrangement of the material. Each major subdivision of Part I has its own introduction, methods, results and discussion sections. In some cases the discussion is quite detailed. In others it contains no more than a comparison of the results with those obtained by other workers on the same animal and the topic will be found to be raised again in a later section. The selection of material for the discussions in the first part of the thesis may appear arbitrary. The policy has, however, been to dispose of matters of technical or limited interest, e.g. the presence or absence of cones in the rabbit retina, within Part I of the thesis. Part II has been reserved for critical and synthetic reviews of various broader topics in visual neurophysiology into which the findings of the experimental work have been introduced. The details of routine experimental methods are given in an Appendix.

Austin Hughes

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I wish to thank my supervisor, Professor D. Whitteridge, for introducing me to visual neurophysiology and for providing space, equipment, help and ideas during the course of the work. I am especially grateful, however, for the considerable freedom which I have been given to pursue my own course of investigation.

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The majority of the experimental equipment was provided by the Medical Research Council to whom I owe thanks.

SUMMARY

A schematic eye is developed for the rabbit and the arrangement of the eyes in the head is discussed in relation to the animal's field of view.

A detailed description of rabbit retinal histology is given which indicates the presence of atypical cones but, in spite of the specialised rabbit retinal units, an otherwise typical mammalian organisation. A quantitative description of ganglion cell density and size distribution is given which clearly illustrates the organisation of the visual streak. The visual streak is also shown to be represented in the bipolar and receptor layers of the retina. An optic nerve fibre count and axon diameter distribution are presented for comparison with the retinal data.

The topography of the projection of the visual field in the superior colliculus, L.G.N. and cortex is developed with one set of experimental techniques. Data is presented on magnification factor and volume representation for all three regions. The relationship of the form of the projection to the organisation of the retina is examined in discussion and a functional interpretation attempted. The differences between rabbit and cat central representation of the visual field are described and the concept of the rabbit as a parallel and the cat as a series visual data processing system is developed. The rabbit is shown to substitute head movements for voluntary eye movements.

The distribution of the callosal projections to the VI/VII border is given and the relation of the cortical visual areas to area 17 and occipitalis is indicated.

The properties of single units in optic nerve, superior colliculus, L.G.N. and visual cortex are described in terms of the results of investigations carried out with similar techniques. An extension of Barlow and Levick's directional unit model is presented, based upon optic nerve data. The optic nerve large field off units are described as projecting to the upper part of the stratum griseum superficiale of the superior colliculus where /

where they may function as an 'early warning system'. The considerable differences between the visual cortex organisation of rabbit and cat is outlined. The universality of the Hubel and Wiesel concept of cortical organisation, which is based upon cat and monkey data, is challenged and the comparative single unit information is examined in detail.

Much space is given to the discussion of comparative retinal unit data. Maturana's concept of deterministic and indeterministic visual systems is considered. The relationship of structure and function in the retina is discussed with respect to various models of unit organisation. Dowling's theory of the seat of visual adaptation is criticised and an alternative offered. The role of the superior colliculus units in the normal animal is discussed but a similar treatment of rabbit visual cortex units is not given because of the inadequacy of the available data.

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PART I

RABBIT EYE AND VISUAL FIELD

INTRODUCTION

The rabbit possesses a highly specialised visual system whose performance is recognised in the natural history and hunting literature as being excellent. An examination of the situation and structure of the eyes reveals certain aspects of the rabbit's adaptation to its way of life in which the early detection of predators is of vital importance. It is, perhaps, the least aggressive of the mammals.

The rabbit is often mistakenly described as nocturnal when it is, in fact, a twilight or crepuscular animal. The well known dawn and dusk activity pattern of the rabbit has been investigated under controlled laboratory conditions by Van Hof, Rietveld and Tordoir (1963). When a natural rhythm of illumination change is applied, the animals show continuous activity around the clock with a peak at dawn and at dusk. If illumination is continuous, they show a peak of activity at night. The time and duration of the period of darkening appears to govern the activity peaks and only when the transition from light to dark is very abrupt does the dark activity peak continue long enough for the animal to be described as nocturnal.

Rods predominate in the rabbit eye but cones are present and may be quite numerous in the region of the area centralis (see p.42). The rabbit possesses a pupil showing slight vertical ovality rather than the slit form common amongst nocturnal animals which are active during the daytime. The eye of the nocturnal animal is usually large relative to the size of the bearer and possesses a large anterior segment, pupil and lens. The lens tends to be spherical and set well back in a fashion which often restricts the visual field and in some cases leads to tunnel vision. The rabbit possesses the large anterior segment and pupil characteristic of the nocturnal types but the lens is intermediate in thickness between the nocturnal and diurnal types. The visual field of the animal is enormous and is achieved by the specialised cornea.

In view of the confusion in the literature concerned with the extent of /

of the rabbit visual field it was decided that some measurements would be carried out and the results of these are described below.

METHODS

Measurements of the monocular field of the excised eye must be attended by inflation of the globe to a pressure of some 28 cm. of water. In order to avoid the difficulties and doubts introduced by this technique an adult eye was dissected out in an anaesthetised animal while its blood supply remained intact. The monocular field was determined by transcleral observation of the retinal image of a small light source moved about in the visual field at a constant distance from the eye. A thread was connected between the source of light and a point on an appropriate axis running through the eye. The intersection of the thread and the scale of a protractor set either above or to the side of the eye enabled the extent of the visual field to be measured in the vertical and horizontal plane. The eye was arranged with its myelinated band horizontal.

Ophthalmoscopic examination of the limits of the light reflex from the retina was used as an alternate method for investigating the extent of the monocular field and also for measurement of the binocular field of the unanaesthetised animal. The latter investigation is readily carried out if the animal is confined in a small box which permits the head to protrude. The head remains motionless in a quiet, dark room for long enough periods for a complete examination with ophthalmoscope and hand perimeter to be carried out.

Photographs of the freshly excised eyes were made in air during inflation with saline from a reservoir with a 28 cm. head.

RESULTS

Anatomy. The plane of the corneo-scleral junction may be seen in the living animal or excised eye to be inclined towards the midline at its superior border. Figure 1A shows this feature as seen from the front. The arrangement /

arrangement extends the upper field at the expense of the lower. The plane of the iris is more tilted than that of the limbus.

In dorsal view (fig. 18) the corneo-scleral junction can be seen to be retracted medially at the nasal and temporal margins. This feature is presumably beneficial in extending the limits of the horizontal monocular field. The cornea is not circular but has a horizontal dimension of 15.6 mm. while in the vertical it extends for only 13.8 mm. on the average (Davis, 1925).

Monocular Field. The monocular field was found, by the method of transcleral illumination, to have a total extent of 195° in the horizontal plane when free of extra-ocular obstructions. The field was symmetrically distributed on each side of the optic axis. In the vertical plane the field was found to extend for only 180° . The method is not necessarily accurate, although generally accepted, for the peripheral scleral thickening at the muscle insertions may prevent viewing of an image which is present.

Observation of the retinal light reflex indicated similar values for the extent of the monocular horizontal and vertical field to those determined by the above technique.

Binocular Field. It should be noted that the extent of the rear field and the frontal binocular field varies with the breed of rabbit examined. The limits of the field are considerably influenced by hair distribution as well as by the eyelid and the ear position. The Dutch rabbit was found to give the most consistent results and demonstrated the largest visual field. The nasal field of each eye was found to extend 15° into the contralateral visual field. At the rear the limit of the field was, at most, parallel with the long axis of the body and often terminated a few degrees lateral of it.

The binocular field began about 30° below the horizontal in the nasal field and extended to 40° beyond the vertical in the midsagittal plane. Immediately above the animal the binocular field is about 30° wide. The 15° medial tilt of the upper vertical field margin, which generates the 30° upper binocular /

binocular field, is complemented by a lateral 15° tilt of the lower vertical margin, which is set at an angle of 180° to it, and thus a blind region exists under the jaw in an area which is screened off by the lateral limits of the head.

DISCUSSION

The monocular field of 195° in the horizontal plane, which is described above, is intermediate in magnitude between the value of 190° quoted by Lindsay Johnson (1901) and that of 198° given by Pisa (1939). The nasal binocular field of 30° is in agreement with the results of Pisa (1939) who found its extent to vary with the emotional condition of the animal from 27° to 32° ; the value presumably being dependent upon the eyelid position. The 10° nasal binocular field described by Lindsay Johnson (1901) is too small. The cortical maps of Thompson, Woolsey and Talbot (1950) show a 20° segment of the nasal monocular field as being represented on the ipsilateral visual cortex which suggests a binocular field more in the order of 40° than 10° .

I was unable to confirm the rear 9° binocular field described by (fig. 2) Lindsay Johnson (1901) and Pisa (1939). No sign of voluntary convergence towards the rear has been observed and the results of the visual cortex mapping do not suggest the presence of a region of enhanced resolution. If the rear limit of the visual field extends parallel to the long axis of the body in the wild rabbit, then effective all-round vision is present because the width of the blind region does not increase with distance from the animal. It is difficult to imagine what benefit would arise from the presence of a rear binocular field because vision in that region would not be stereoptic as corresponding cortical points are not superimposed.

The results are summarised in fig. 3 which is a schematic diagram of the rabbit visual field constructed from the observed monocular fields by means of the orthographic transformation technique described in the section on methods. The reason for the slight difference between this diagram and the observed field is described in the accompanying legend. The overlap of the /

the monocular fields above the animal is described as generating a binocular field only in the sense that a retinal light reflex may be observed from both eyes in this region of the visual field. The functional significance of the region can be discussed only in conjunction with observations on more central regions of the visual system .

The projection of the blind spot of the rabbit is shown in fig. 3 as a band shaped region of the visual field . The blind spot itself may be seen in the accompanying photograph of an eye opened and photographed under saline (fig. 1C). The optic nerve fibres fan out both nasally and temporally and remain myelinated until they branch off to their destinations. The band is positioned so as to project into the lower visual field about 20° below and parallel to the horizontal. The projection of the band is about 140° long by 8° wide and offers little impediment to predator detection. This is an important feature in animals with lateral eyes for there is no complementary coverage of the blind region by the other eye.

Fig. 1 A. Frontal view of the right eye showing medial inclination of the corneo-scleral boundary. The arrow indicates the point of entry of the optic nerve head.

B. Dorsal view of the right eye. The corneo-scleral boundary is slightly retracted on each side. The angle between the right and left margins is about 190° .

C. The eye cup opened and photographed under saline showing the optic nerve head marked by the arrow and the myelinated fibres fanning out to each side.

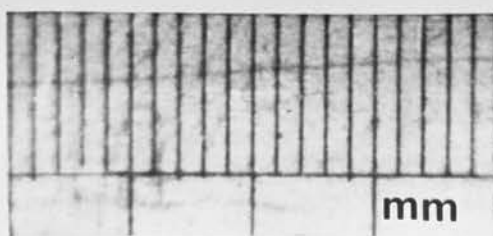
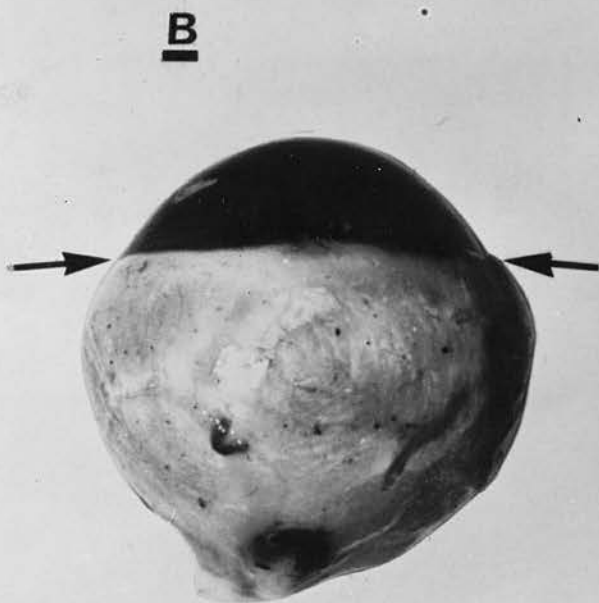
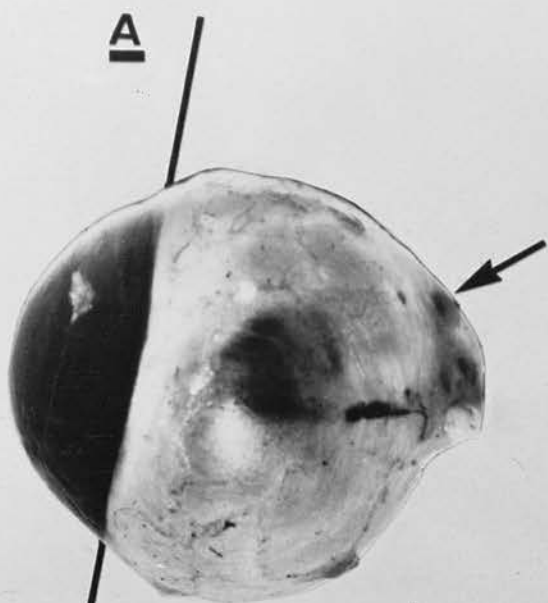
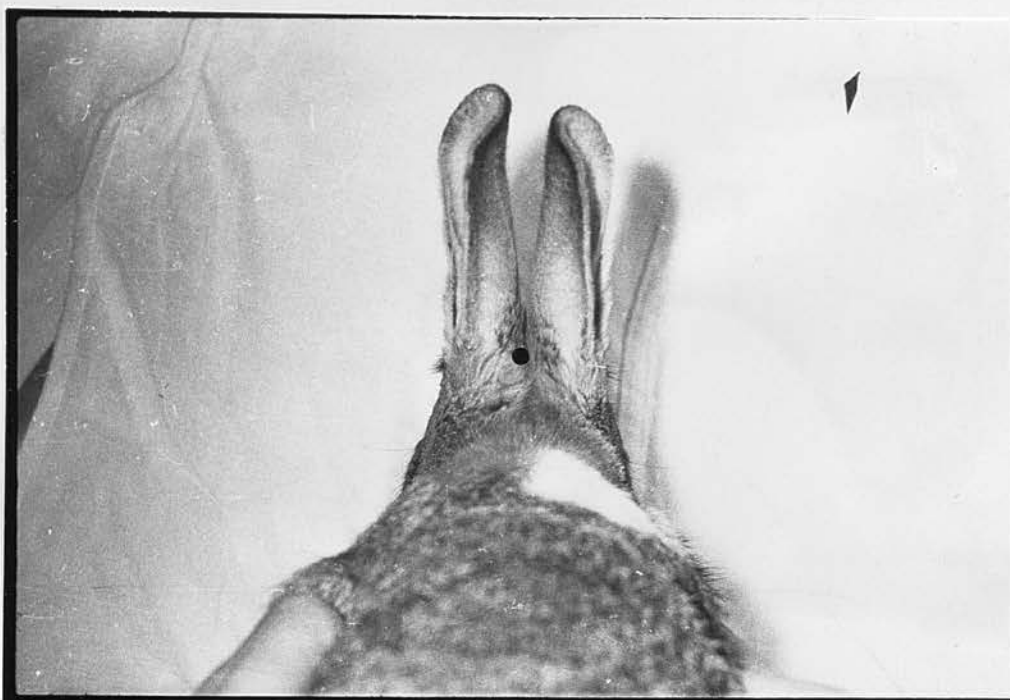


Fig. 2 A. Short haired rabbit photographed from behind to test for the presence of a rear binocular field. The black spot indicates that the camera frame is centred between the animal's eyes. At a distance of nearly three feet neither cornea is visible.

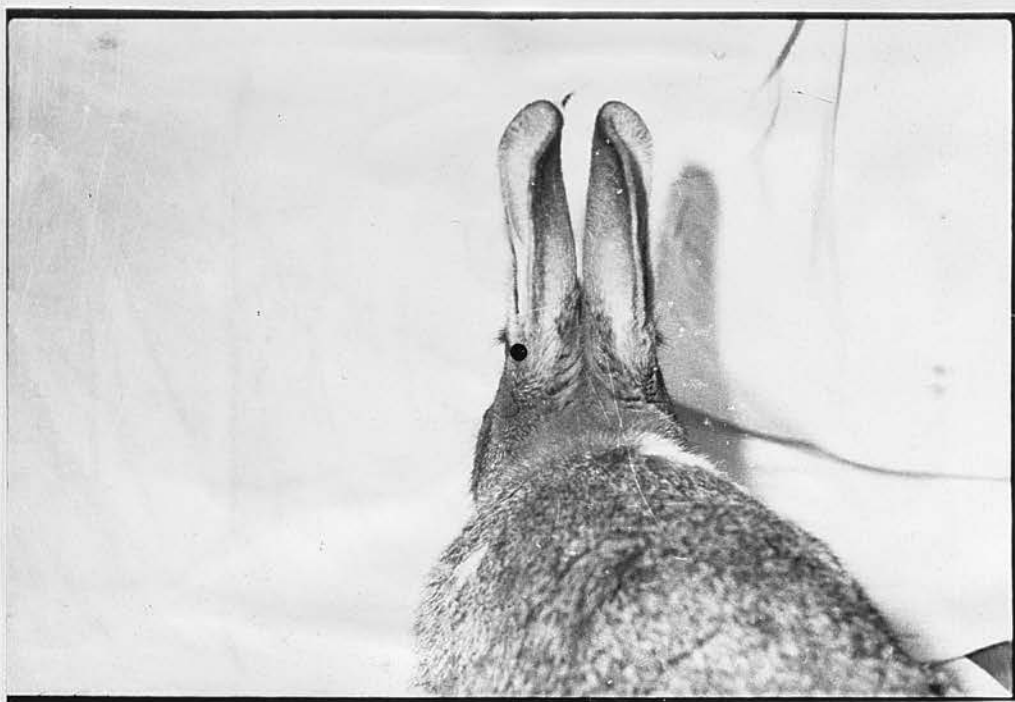
B. This frame is centred at the middle of the animal's left eye. Only the vertex of the left cornea is visible. Viewed ophthalmoscopically this would just be inadequate to obtain a light reflex.

It is clear that this animal cannot possess any useful binocular overlap behind its head. It appears most likely that the limits of the rear field for right and left eye run back parallel to each other behind the animal.

If a 10° rear binocular field existed as is claimed in the literature, then the cornea should appear in photographs like 1A at distances greater than 1 foot from the head of the rabbit.



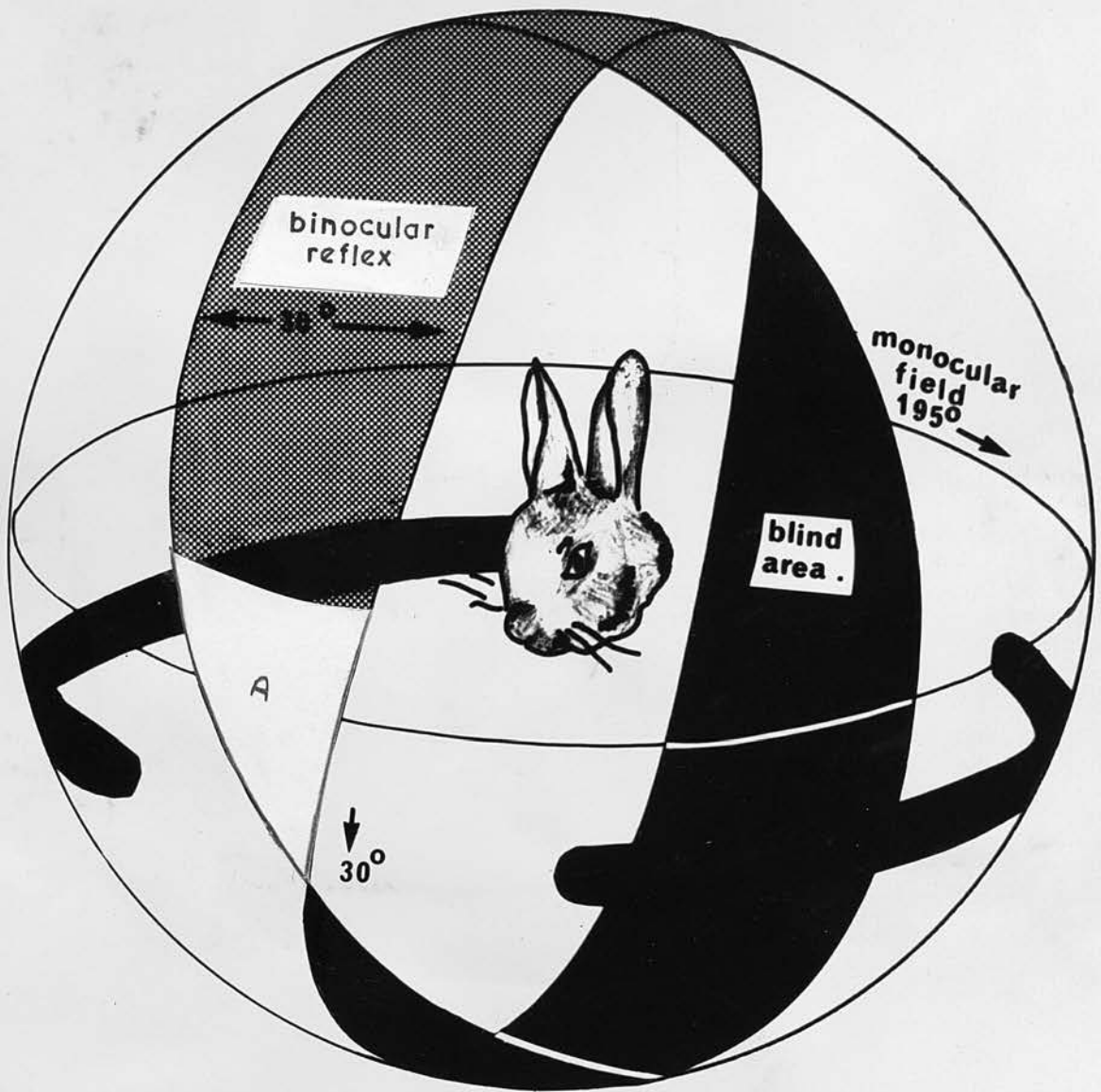
A



B

Fig. 3 A schematic diagram showing the visual field of the rabbit. The observer views along an axis orientated 15° to the left of the antero-posterior axis and 15° above the horizontal parallel. The diagram was constructed by nomographic transformation of the two schematic monocular field envelopes inclined towards each other at an angle of 15° . Obstruction of the field by the body is not considered in delineating the blind area. The projection of the myelinated band gives rise to a blind streak in the lower part of each monocular field.

The region A is the binocular field which has been confirmed as such in the central representation. It appears foreshortened in this projection but reaches 30° below the horizontal and is wider in its lower part than this construction indicates. The hatched area in the upper field is that from which a binocular light reflex may be obtained ophthalmoscopically. The central representation of this region has not so far been recorded from and it may not yet be regarded as functionally binocular. The extent of this area depends upon the lid position and extent of eye protrusion which is variable in the rabbit.



THE RABBIT SCHEMATIC EYE

INTRODUCTION

Work on the optics of the eye has been almost entirely confined to man. The authors of a recent and exhaustive study of the cat eye have commented upon the lack of data available in the literature (Vakur, Bishop, Kozak, 1963). Lashley (1932) has treated rat optics but does not provide a schematic eye.

The anatomy of the rabbit eye has been qualitatively examined in some detail (Davis, 1929; Sheppard, 1961). A number of papers are available which present quantitative information about the components of the rabbit optical system but it has not yet been used for the calculation of a schematic eye. A recent, 650 page, volume devoted to the rabbit eye does not contain a discussion of its optics (Prince, 1964).

The model eye which is subsequently developed is based on the computing schedule described by D. A. Gullstrand in the English translation of Helmholtz's 'Handbuch der physiologischen Optik' (1909-1911). The calculation has, however, been simplified by the assumption of a homogeneous lens.

The power of the rabbit cornea and lens undergoes considerable change in the first 30 weeks of life. These changes are probably the necessary concomitant of the increase in size of the eye during growth. The medio-lateral axial dimension of the newborn rabbit eye is about 6 mm.; the adult value is in the order of 18.5 mm. The human eye undergoes an axial elongation of only 6 mm. in post-natal growth. In selecting optical data from the literature it is consequently necessary to ensure that young rabbits were not used as experimental material. The values used in the ensuing pages were determined by observations on the eyes of animals older than 80 weeks or weighing more than 2.5 kg. A set of measurements made on a single population would clearly be more satisfactory.

Calculation of the schematic eye begins with the use of thick lens theory to develop an equivalent thin lens for the cornea and for the crystalline lens. The calculation is completed when a further thin lens is derived to represent the behaviour of the whole eye by the combination of the equivalent /

equivalent thin corneal and crystalline lenses. The model is valid for axial rays alone.

THE CORNEA

Data. Vakkur and Bishop (1963) assume the refractive index of the cat cornea to be the same as the value accepted for man (1.376) in Gullstrand's schematic eye. An Abbe refractometer was used to determine the refractive index of the rabbit cornea immediately after its removal from an anaesthetised animal. The measurements were carried out at room temperature. The average of measurements made on three animals was 1.376 to three significant figures. The value may be justified for application to the intact living eye by back calculation from the measured total corneal power and the known corneal radii of curvature.

Valentin (1879) reports a value of 1.337 as the refractive index of the rabbit aqueous humour. Freytag (1910) obtained a range of values from 1.33-1.329 for animals of between 9 days and 5 years of age. Samples of fresh aqueous humour withdrawn from the anterior chamber by hypodermic syringe gave an average value of 1.337. This latter value will be used in the ensuing calculations.

The radius of curvature of the anterior corneal surface has been measured by several workers; Prince (1964) quotes 7.0-7.5 mm.; Davis (1929), 7.3 mm.; Sorsby and Sheridan (1953), 7.5-8.25 mm. Keratometer measurements carried out by the author gave readings from 7.3-7.8 mm. on adult rabbits. For the following calculations the anterior corneal radius of curvature has been assumed to be 7.5 mm.

The inner corneal surface has been assumed to be concentric with the anterior surface. Its radius of curvature is less than that of the anterior surface by the apical corneal thickness. The reader is referred to Prince (1964) for a discussion of corneal thickness - a value of 0.4 mm. is assumed here.

The following conventions are observed in the ensuing calculations.
Light /

Light rays enter the system from left to right; the refractive indices of the media encountered are numbered in the same direction beginning with air, n_1 ; surfaces are numbered in the order encountered, beginning with the anterior vertex of the cornea, A_1 , which is used as a reference point for the measurement of distances. Measurements to the right of A_1 are positive. Surfaces convex to the light are defined as having positive radii of curvature (r). The first principal point of a system is indicated by a suffixed capital letter, e.g. H_{12} ; the second principal point is represented similarly but bears an apostrophe.

Calculation. The refracting power of the anterior surface of the cornea is

$$F_1 = \frac{n_2 - n_1}{r_1} = \frac{(1.376 - 1) \times 10^3}{7.5} = +50D \quad (1)$$

and that of the posterior surface is

$$F_2 = \frac{n_3 - n_2}{r_2} = \frac{(1.337 - 1.376) \times 10^3}{-7.1} = -5.5D \quad (2)$$

The reduced interval (Gullstrand, 1924) between the two surfaces is

$$C_1 = \frac{A_1 \cdot A_2}{n_2} = \frac{4.0 \times 10^{-4}}{1.376} = 2.9 \times 10^{-4} m \quad (3)$$

If F_{12} denotes the refracting power of the corneal system where

$$F_{12} = F_1 + F_2 - C_1 \cdot F_1 \cdot F_2 \quad (4)$$

then

$$F_{12} = 50 - 5.5 - 2.9 \cdot 10^{-4} \cdot 50 \cdot (-5.5) = 44.4D \quad (5)$$

The principal points of the cornea system are given by

$$A_1 H_{12} = \frac{C_1 \cdot F_2}{F_{12}} = \frac{2.9 \cdot 10^{-4} \cdot (-5.5)}{44.4} = -0.36 \cdot 10^{-4} m \quad (6)$$

We assume H_{12} to be equal to A_1 .

$$A_2 H'_{12} = -\frac{C_1 \cdot F_1 \cdot n_3}{F_{12}} = \frac{-2.9 \cdot 10^{-4} \cdot 1.337 \cdot 50}{44.4} = -4.37 \times 10^{-4} m \quad (7)$$

and thus $A_1 H'_{12} = -0.04 mm$. We assume that H'_{12} is at A_1 .

The schematic corneal power of 44.4D is in quite good agreement with published values for the adult rabbit. Stone and Leary (1957) report that the corneal power stabilises at 42D in the 60th post-natal week. Chou (1954) reports a final value of 45D attained after 40 weeks while Sorsby, Benjamin, Sheridan, Davy and Tenner (1957) find 43D to be average value for adult British rabbits.

THE CRYSTALLINE LENS

Data. The crystalline lens lies 2.9 mm. behind the posterior corneal surface. This distance is achieved in the 20th post-natal week and afterwards remains constant (Sorsby, Stone, Leary & Sheridan, 1960) (fig. 3).

The anterior radius of curvature of the lens reaches a value of 7.0 mm. in the 60th post-natal week and remains constant afterwards (Sorsby et al., 1960). Keratometer measurements on the excised lenses of rabbits weighing more than 2.5 kg. are less satisfactory than those which Sorsby et al. obtained from the intact eye by photographic ophthalmophakometry but are essentially in agreement. Measurements on three rabbits gave readings of 7.1, 7.0 and 6.7 mm. The value of 5.0 mm. suggested by Prince (1964) is very low.

The lens of the rabbit eye is rather thick; Prince (1964) reports a value of 7.0 mm. My own measurements, which were conducted with the lens immersed in vitreous humour in order to reduce distortion, suggest a higher value. A range from 7.0 to 8.6 mm. was obtained. Sorsby et al. (1961) do not give details but mention a range from 8.0 to 10.0 mm. The average of six measurements made on our own animals will be used (7.5 mm.).

The radius of curvature of the rear surface of the lens is not readily obtained from the intact eye because of the thickness of the lens. Prince suggests a value of 5.0 mm. Measurements made on the excised lens gave an average value of 5.2 mm.

The crystalline lens consists of a capsule which contains a core of rather higher refractive index. Valentin (1879) gives the value of 1.448 for the lens core; Freytag described a range from 1.417 to 1.465 for animals from 9 days to 5.5 years of age (1910). Freytag found the index to vary more in rabbits between the young and the old individual than in any other animal he investigated.

The Abbe refractometer has been used to measure the refractive index of both capsule and core in the present investigations. The capsule, when blotted dry, gave readings ranging from 1.407 to 1.412. The core gave readings /

readings from 1.43 to 1.46. These readings are included for the sake of completeness rather than for use in the schematic eye calculations. The gradient of refractive index through the lens makes it impossible to develop a schematic eye with the simple lens formulae. The effect of the core is to increase the power of the lens relative to a homogeneous lens of the same refractive index as the core. It is thus possible to represent the lens by an equivalent organ of identical shape but of uniform and higher refractive index. The refractive index of the equivalent, homogeneous, lens is known as the total or overall refractive index of the lens. The literature appears to contain no measurements of the total refractive index of the rabbit lens. Sorsby (1961) et al. give reasons to support the view that it is about 1.6. An estimate of its value was obtained in the following fashion.

The distance from the posterior vertex of the lens to the posterior focal point was measured. A small source of light was placed at a distance of two meters in front of the excised lens; the image of the source was focused on a screen affixed to the end of a micrometer placed behind the lens. The micrometer reading was taken at the position of best focus and at the posterior vertex of the lens. The inverse of the difference between these two readings may be taken, without much error, to be the back vertex power of the lens in air (expressed in diopters when the distance is measured in meters). An average reading for six lenses was 3.7 mm. to one decimal place. The back vertex power in air is thus 270D.

In order to test the suggested value of 1.6 for the lens refractive index we now assume the figure and use thick lens theory to calculate the back vertex power in air. A good agreement between the theoretical and experimentally determined values will justify the assumed refractive index.

Calculation. Using parameters averaged from six lenses we have for the anterior surface power of the lens in air,

$$F_{3a} = \frac{(n_4 - n_1) \times 10^3}{r^3} = \frac{(1.6 - 1) \times 10^3}{-1.0} = 26D \quad (1)$$

The /

The posterior surface power is given by

$$F_{4a} = \frac{n_1 - n_4 \times 10^{-3}}{r_4} = \frac{(1 - 1.6) \times 10^3}{-5.2} = 115 \text{ D} \quad (1)$$

Thick lens theory gives the posterior vertex power as

$$F'_{va} = \frac{F_{3a} + F_{4a} - \frac{t}{n_4} F_{3a} \cdot F_{4a}}{1 - \frac{t}{n_4} F_{3a}} = \frac{86 + 115 - \frac{7.5}{1.6} \cdot 10^{-3} \cdot 86 \cdot 115}{1 - \frac{7.5}{1.6} \cdot 10^{-3} \cdot 86} \approx 260 \text{ D} \quad (2)$$

The agreement between the theoretically determined 260D and the measured 270D is close enough to justify the use of the value 1.6 for the total refractive index of the lens.

We may now calculate the equivalent thin lens for the crystalline lens immersed in aqueous and vitreous humours. For the anterior surface power we have

$$F_3 = \frac{(n_4 - n_3) \times 10^3}{r_3} = \frac{(1.6 - 1.337) \times 10^3}{7.0} = 37.6 \text{ D} \quad (3)$$

For the posterior surface power

$$F_4 = \frac{(n_5 - n_4) \times 10^3}{r_4} = \frac{(1.337 - 1.6) \times 10^3}{-5.2} = 50.5 \text{ D} \quad (4)$$

If the refracting power of the lens system as a whole is denoted by L, then

$$L = F_3 + F_4 - s \cdot F_3 \cdot F_4 \quad (5)$$

where the reduced thickness is denoted by s,

$$s = \frac{7.5 \times 10^{-3}}{1.6} = 4.7 \times 10^{-3} \quad (6)$$

we find that

$$L = 37.6 + 50.5 - 4.7 \times 10^{-3} \cdot 37.6 \cdot 50.5 \approx 79 \text{ D} \quad (7)$$

The primary principal point of the lens system, H_{34} , is given by

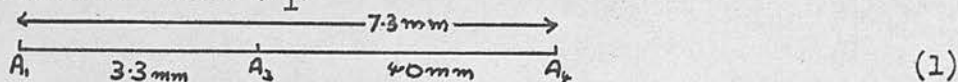
$$\frac{A_3 H_{34}}{n_3} = \frac{s F_4}{F_{34}} \therefore A_3 H_{34} = \frac{4.7 \cdot 10^{-3} \cdot 50.5 \cdot 1.337}{79.0} = 4.0 \times 10^{-3} \text{ m} \quad (8)$$

The second principal point, H'_{34} , is given by

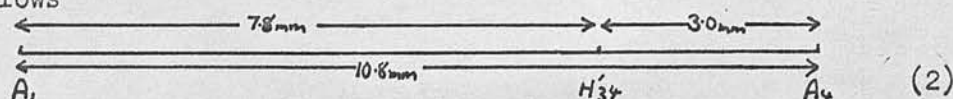
$$\frac{A_4 H'_{34}}{n_3} = -\frac{s F_3}{F_{34}} \therefore A_4 H'_{34} = -\frac{4.7 \cdot 10^{-3} \cdot 37.6 \cdot 1.337}{79.0} = 3.0 \times 10^{-3} \text{ m} \quad (9)$$

The first principal point of the lens lies in the following relationship to the /

the anterior corneal vertex (A_1)



so that $A_1 H'_{34}$ is 7.3 mm. The second principal point lies in relationship to A_1 as follows



so that $A_1 H'_{34}$ is 7.8 mm.

THE SCHEMATIC EYE

Calculation. We are now in a position to combine the cornea and lens systems to obtain the parameters of the schematic eye. The refracting power of the optical system of the whole eye is given by

$$F = F_{12} + L - C \cdot F_{12} \cdot L \quad (3)$$

where the reduced distance c is the distance between the second principal point of the corneal system and the first principal point of the lens system divided by the refractive index of the aqueous humour. H'_{12} is at A_1 so

$$C = \frac{H'_{12} H_{34}}{n_3} = \frac{A_1 H_{34}}{n_3} = \frac{7.3 \times 10^{-3}}{1.337} = 5.46 \times 10^{-3} \text{ m} \quad (4)$$

and

$$F = 44.4 + 79 - 5.46 \cdot 10^{-3} \cdot 44.4 \cdot 79 = 104 \text{ D} \quad (5)$$

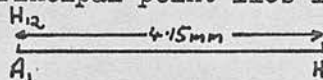
The first principal point of the schematic eye is given by

$$H_{12} H = - \frac{C \cdot L \cdot n_1}{F} = \frac{5.46 \cdot 10^{-3} \cdot 79 \cdot 1}{104} = 4.15 \times 10^{-3} \text{ m} \quad (6)$$

The second principal point is given by

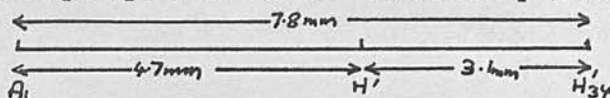
$$H'_{34} H' = - \frac{C \cdot F_{12} \cdot n_2}{F} = \frac{5.46 \cdot 10^{-3} \cdot 44.4 \cdot 1.337}{104} = 3.1 \cdot 10^{-3} \text{ m} \quad (7)$$

The first principal point lies in the following relationship to A_1



so that $A_1 H$ is 4.15 mm.

The second principal point lies in relationship to A_1 as follows



so that A_1H' is 4.7 mm.

If the focal lengths of the eye are denoted by f and f' we have

$$f = \frac{n_1}{F} = \frac{1}{104} = 9.6 \text{ mm} \quad (1)$$

and

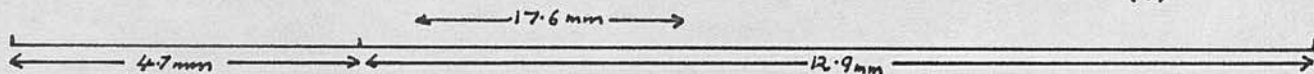
$$f' = -\frac{n_5}{F} = -\frac{1.337}{104} = -12.9 \text{ mm} \quad (2)$$

The focal points P and P' are thus located as follows

$$A_1H - f = A_1P = 4.15 - 9.6 = -5.45 \text{ mm} \quad (3)$$

and

$$A_1P' = A_1H' - f' = 4.7 - (-12.9) = +17.6 \text{ mm} \quad (4)$$



CONCLUSIONS

Refractive State of the Rabbit Eye. The refractive condition of the rabbit schematic eye cannot be ascertained without an estimate of the distance, along the optic axis, of the photoreceptor layer from the anterior corneal vertex. Rochon-Duvigneaud (1943) has given a mediolateral measurement for the globe of 17-18 mm. Land (1957) has published a table of globe dimensions for animals of various ages. The average of the mediolateral dimension of ten eyes from rabbits weighing more than 2.5 kg. is given as 18.5 mm. for the American animal which is larger than the European. Sheppard (1961) quotes the globe as being 17-18.5 mm. in the mediolateral dimension. Sorsby et al. (1960) find the average adult mediolateral globe dimension to be 18.0 mm. for rabbits in this country. The mediolateral dimension of the globe was determined by micrometer for six excised rabbit eyes /

eyes after they had been inflated to an internal pressure of 30.0 cm. of water. The average of the results was 18.1 mm. We assume that the adult eye is 18.0 mm. in its mediolateral dimension.

The image should be brought to a focus at the photoreceptor layer, which is some distance in front of the posterior scleral surface. The scleral thickness varies considerably but under the visual streak, or region of high ganglion cell concentration, the sclera is less than 0.2 mm. thick (Prince, 1864). In the same area, the choroid reaches a maximum thickness of about 0.1 mm. in freshly cut material (Sheppard, 1964) but in the living animal it must readily attain a dimension twice as great when full of blood (Valkur et al., 1963). We thus take the combined thickness of the choroid and sclera to be 0.4 mm. The distance from the anterior vertex of the cornea to the pigment layer which backs the photoreceptors is thus 17.6 mm.

The calculated posterior focal length of the schematic eye is 17.6 mm. (equation 4 on previous page) which is identical to that obtained for the photoreceptor position from anatomical considerations. This perfect agreement is admittedly engineered but only in the choice of the increase in choroidal thickness introduced to allow for the presence of blood in the living tissue. Even without this allowance the schematic eye has an out of focus distance of only 0.1 mm. The schematic eye thus predicts that the rabbit eye should be emmetropic. Reference to the literature substantiates this prediction but it is clear that there are quite considerable variations in the refractive state of different populations of adult animals.

Duke-Elder (1958) describes the wild rabbit as being hypermetropic but suggests that, in captivity, there is a tendency for the animal to become myopic. Thompson (1953) found the eye of the anaesthetised rabbit to be about 4D hypermetropic. More extensive investigations of the change in refraction during growth have been conducted by Chou (1954) and Stone and Leary (1957). The animals used by Chou were emmetropic after their 40th week while those investigated by Stone and Leary stabilised at about 2D of hypermetropia. The difference may well result from their use of different populations /

TABLE I

Schematic Eye of the Rabbit.

Refractive Index				
Cornea	n_2	1.376		
Aqueous and Vitreous	n_3 n_5	1.337		
Lens (Total index)	n_4	1.6		
Dimensions				
Surface		Position (mm)	Radius (mm)	
Anterior corneal	A_1	0.0	7.5	
Posterior corneal	A_2	0.4	7.1	
Anterior lenticular	A_3	3.3	7.0	
Posterior lenticular	A_4	10.8	-5.2	
Receptor	A_5	17.6	-	
Posterior scleral	A_6	18.0	-9.6	
Powers (D)				
	Cornea		Lens	Whole eye
Anterior surface power	F_1 50.0		F_3 37.6	-
Posterior surface power	F_2 -5.5		F_4 50.5	-
Total power	F_{12} 44.4		L 79.0	103
Distances (mm)				
Anterior focal length	-		-	f 9.6
Posterior focal length	-		-	f' -12.9
First principal point	A_1H_{12} -0.036		A_3H_{34} 4.0	$H_{12}H$ 4.15
Second principal point	A_1H_{12}' -0.44		A_3H_{34}' 3.0	$H_{12}H'$ 4.7
Distances from A_1 (mm)				
Anterior principal point	H_{12} -0.036		H_{34} 7.3	H 4.15
Posterior principal point	H_{12}' -0.44		H_{34}' 7.8	H' 4.7
Anterior focal point	-		-	F -5.45
Posterior focal point	-		-	F' 17.6
Anterior nodal point	-		-	N 7.5
Posterior nodal point	-		-	N' 8.0
Posterior nodal distance 9.6 mm				
Refraction ≈ 0				

populations of animals. Gardiner and MacDonald (1957) found that a reduction in the protein intake of young rabbits slows their growth and increases their hypermetropia; return to a balanced diet brings about a return to emmetropia. Most of the animals used in this laboratory have been found to be within 1D and inevitably within 2D of emmetropia before and after anaesthesia (direct ophthalmoscopy). Only rarely are myopic animals encountered.

The Monocular Field of View. The observed monocular field of the rabbit has already been described. It is possible to use the schematic eye to calculate the limits of this field. A light ray, incident upon the lens, whose extension into the lens intersects the equatorial margin will be refracted into the vitreous humour. Thus, in figure 5, the ray enters at the corneo-scleral junction and has an angle of refraction of 16° . Assuming that the cornea is a single refracting surface of refractive index 1.38, we find the angle of incidence to be 22.5° . Assuming symmetry of the eye, then this leads to a minimum field of 185° . The limit of the field is given by ray B which grazes the lens tangentially and cannot enter. This ray must have an angle of incidence of 52° so that the total field must be less than about 244° . The actual critical angle depends greatly upon the situation of the lens and pupil relative to each other and the form of the corneo-scleral junction. These factors have not been determined sufficiently accurately for further calculation to be profitable. It suffices that the actual monocular field does lie between the values suggested above.

Image Formation. The adult rabbit eye has been shown to be nearly emmetropic. During experiments to be described later, in which the visual receptive fields of single units were explored, it was necessary to protect the cornea from drying out by fitting a contact lens. Visual stimuli were presented against the background of a plane surface tangential to the surface of a sphere centered at the anterior nodal point of the eye. In the early experiments this was 33 cm. from the eye and was later moved back to 66 cm. It is necessary to consider the extent of image blurring when working at such short distances. The process is facilitated by the use of a rather more /

more simple schematic eye.

The Emsley reduced eye consists of a single refracting surface situated at a distance behind the cornea equal to that of the midpoint between the first and second principal points (4.43 mm.). The center of curvature of the surface falls at the midpoint between the anterior and posterior nodal points (7.73 mm.). The radius of curvature of the surface is thus 3.3 mm. Assuming the medium of the reduced eye to be of refractive index 1.34, we find the power of the surface to be

$$F_r = \frac{(n_2 - n_1) \cdot 10^3}{r} = \frac{(1.34 - 1) \cdot 10^3}{3.3} = 103 \text{ D} \quad (1)$$

The posterior focal length of the system is

$$1.34 \cdot (1/103 \text{ D}) \text{ mm} = 13.0 \text{ mm} \quad (2)$$

This distance is measured from the refracting surface so that the image is formed a further 4.43 mm., or a total of 17.33 mm., behind the cornea.

An emmetropic eye must accommodate by $1/X \text{ D}$ to bring an object $-X$ meters in front of the principal point to a focus. If accommodation does not occur, then the blur circle of the retinal image of a point source will be of the same diameter as that of a distant point source whose parallel rays enter an ametropic eye whose refraction K is equal to the necessary accommodation ($1/X \text{ D}$) mentioned above. The diameter of the blur circle of such a distant source may be shown to be

$$b = \frac{p K}{K + F_r} \quad (3)$$

for the Emsley reduced eye where b is the diameter of the blur circle; F_r is the power of the eye and p is the diameter of the pupil.

The pupil was not deliberately dilated during the experiments and was usually 5-7 mm. in diameter. Assuming the latter value, we find that the blur circle of a source at 33 cm. is given as

$$\frac{7 \times 3}{3 + 103} = 0.2 \text{ mm} \quad (4)$$

and at 66 cm. as

$$\frac{7 \times 1.5}{1.5 + 103} = 0.1 \text{ mm} \quad (5)$$

The schematic eye indicates these values to be about 1.2° and 0.6° respectively. Such values are quite large when compared with the single unit fields of some of the optic nerve fibres. It is conceivable that such a refractive error might prevent the detection of units which respond only to sophisticated stimuli such as a narrow bar of certain width.

Barlow and Levick (1965) have shown that deliberately introduced refractive errors have little effect on the response of directional units. With a pupil 8 by 6 cm. it was shown that a directional response was obtained from the movement of bars, as narrow as 20 ft. of arc, over a 12D range of hypermetropia. The reduction of pupil diameter to 3 mm. extended the range to some 20D. The stimuli used in the experiments described below were rarely less than 0.5° in their least dimension.

During one experiment, a long field unit of the colliculus was examined after the introduction of auxiliary lenses in the spectacle plane. Movements of a black disc 5° in diameter failed to cause a response outside the range of +3D to -2D.

The results suggest that considerable attention should be paid to ensuring the addition of sufficient spectacle power to accommodate the preparation's eye to objects in the stimulus plane. Adjustment for near vision is readily applied in the contact lens routinely used to protect the eye from drying. In order to avoid the need for a range of lenses artificial pupils or myotics might be resorted to as the general illumination level is quite high during experiments.

The Aphakic Rabbit Eye. Prince (1964) reports Chanturishvilli and Stenhouse (1960) as finding the rabbit eye to become 10D hypermetropic upon removal of the lens. The latter authors appear to assume that the rabbit and human lens contribute the same amount to the total power of the eye. Their observation of a 10D change in the power of the eye was made upon animals in which the lens core had been removed while the capsule remained in place. As long as other factors did not intervene, it may be that the capsule contributed enough power to prevent the expected change of about 30D. The /

The power of an emmetropic aphakic rabbit eye must be

$$\frac{1.237 \times 10^3}{17.6} = +76D \quad (1)$$

The corneal power has already been given as 44.5D. The refractive error of the completely aphakic eye is thus

$$76 - 44.5 = +31D \quad (2)$$

The observations of Chanturishvilli and Stenhouse are thus not in accord with this simple calculation which is based upon the well established corneal power and mediolateral globe dimension.

Retinal Visual Field Projection. The calculation of the retinal arc representing two points one degree apart in the visual field is a necessary preliminary to the examination of the transformation of the visual field projection at various levels in the C.N.S. For this we require a schematic parameter which has not yet been mentioned - the posterior nodal distance.

The eye is an unequifocal system because the refractive index of the first and last media is different. The principal points thus no longer possess the property of being the axial points at which the object and image subtend equal angles. This property now belongs to the axial nodal points. Any paraxial ray incident on the first nodal point will emerge from the system as though from the second nodal point (N') and will be parallel to the incident ray. The positions of the nodal points are simply derived

$$NF = H'F' = f' = -12.9 \text{ mm.} \quad (1)$$

$$N'F' = HF = f = +9.6 \text{ mm.} \quad (2)$$

The latter measurement is the posterior nodal distance which should coincide with the center of curvature of the retina. The eye in figure 4 has a radius of curvature of about 10 mm. Subtracting the thickness of sclera and choroid gives a value of 9.6 mm. for the radius of curvature which thus corresponds with the schematic value.

Thompson's measurement of 5.7 mm for the FND of the rabbit appears to be the only directly determined value available in the literature (1953).

The /

The figure is considerably different from that predicted by the schematic eye. A measurement of the FND was consequently made on a number of freshly excised eyes inflated to a pressure of 30 cm. of water by means of a large hypodermic needle inserted into the vitreous and connected to a saline reservoir of adjustable height. A small light source was placed 100 cm. in front of the eye and moved 20 cm. along a line tangent to the radius connecting it to the eye. The retinal image of the light was observed transclerally through a travelling microscope and the chordal displacement measured. In the case of small movements of the light it is possible to obtain the FND, by similar triangles, from the ratio of the chordal displacements.

The average of five measurements on the equator of the globe and near to the optic axis gave a retinal image displacement of 1.9 mm. for a 20 cm. movement of the source. The FND is thus

$$\frac{1.9}{200} \times 1,000 = 9.5 \text{ mm} \quad (1)$$

and is in agreement with the schematic eye. It would appear that Thompson used a very young rabbit.

A FND of 9.5 mm. means that, in the emmetropic eye, one degree in the visual field is represented by

$$\frac{2\pi \cdot 9.5}{360} = 0.165 \text{ mm/}^\circ \quad (2)$$

on the retina (assuming the equality of the chordal and circumferential displacements). Both schematic eye and experiment agree in setting this figure.

During the same experiments some observations were made on the retinal representation of the visual field at points away from the optic axis. For at least 45° above and below the equator of the globe the retinal scale was unchanged at about 0.165 mm/°. This value also applied for some 50° nasal and temporal along the equator. At the equator, in the nasal and temporal limits of the field, (some 60° out from the optic axis) the value dropped to 0.13 mm/°, a change of about 20%.

The /

The interference with the eye that is necessary for the performance of the above experiment makes it rather unsatisfactory. The visual field could readily be mapped on to the retina by the use of a laser ophthalmoscope but, as yet, such an instrument has not been accessible for this purpose.




Fig. 4 A. The eye photographed in dorsal view under saline to reveal the cornea, c; lens, l; and iris, i.

B. A photomontage showing an excised lens in its correct position in the above eye.

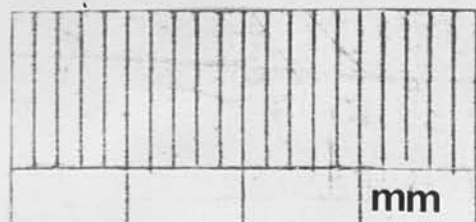
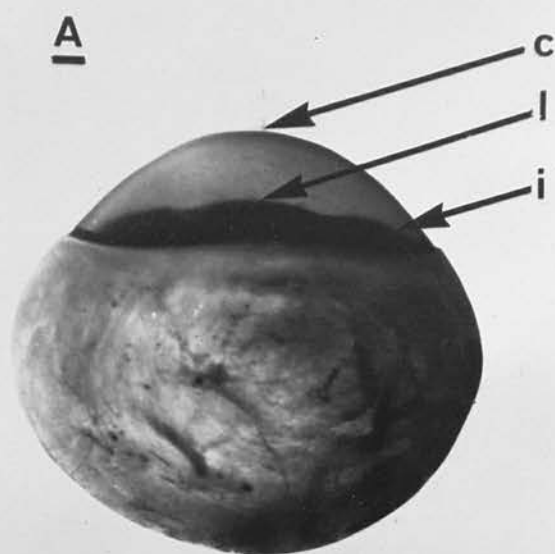


Fig. 5 The limits of the monocular field estimated from the schematic eye. The diagram is explained in the text on page 15.

scale
0 5mm

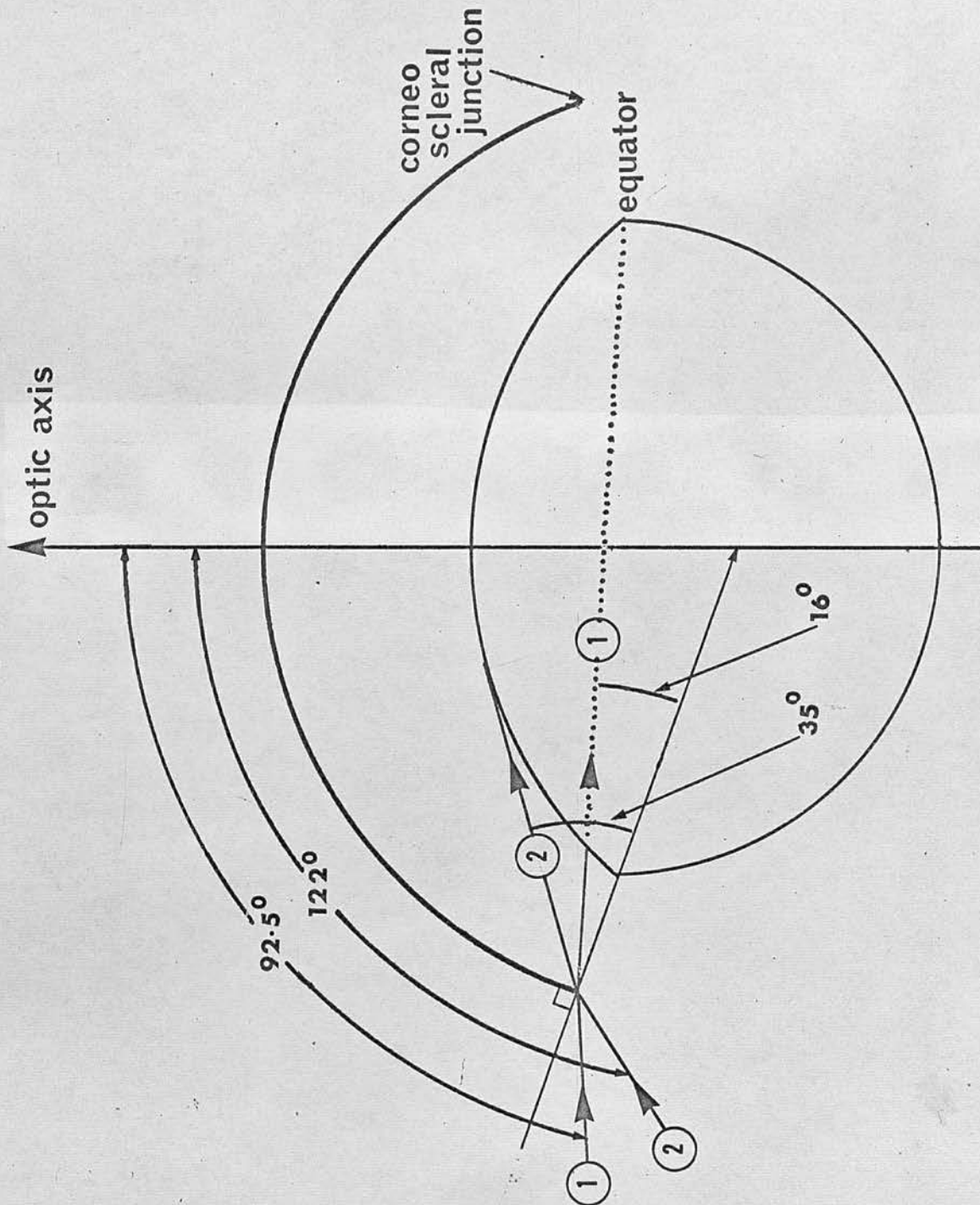
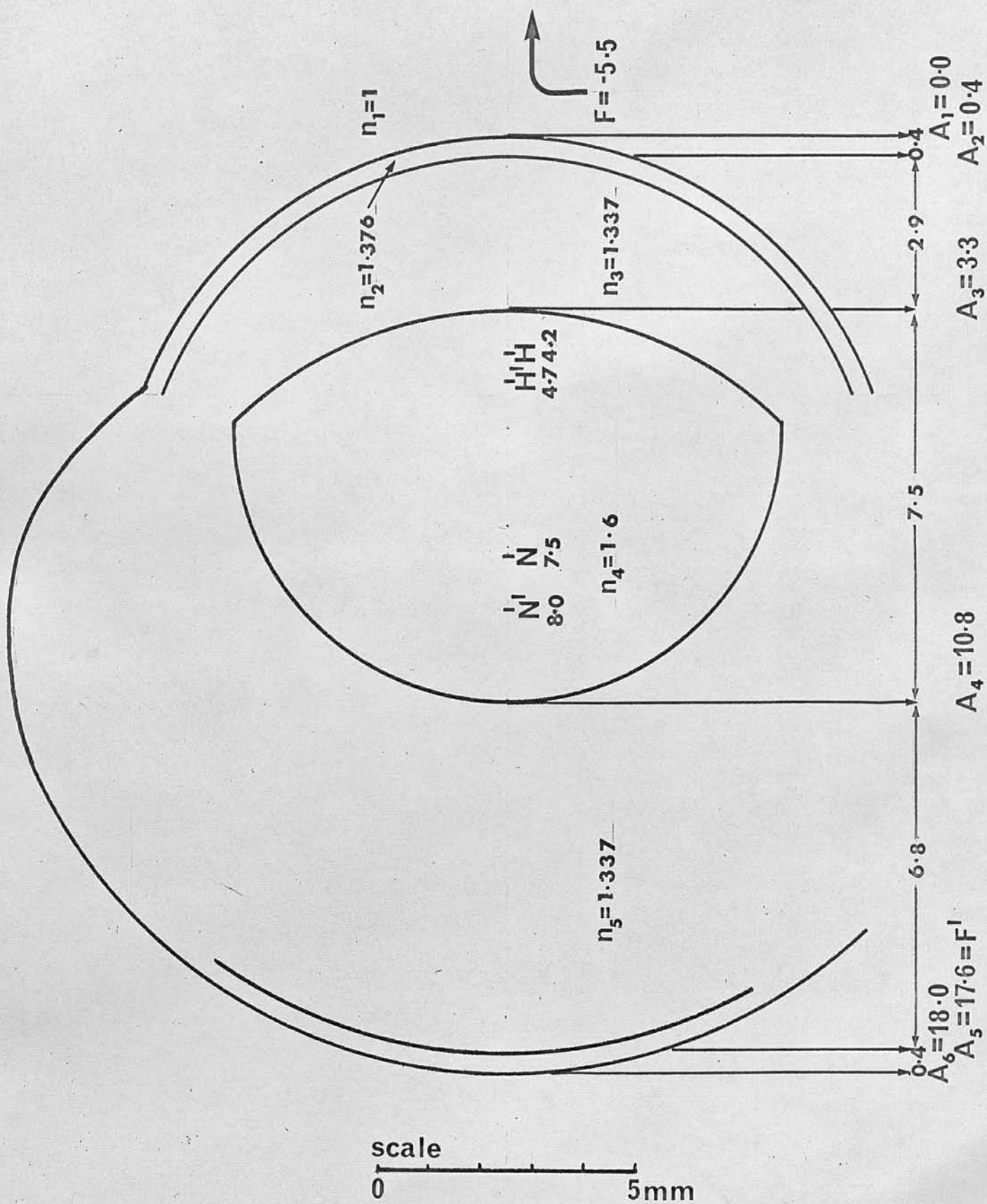


Fig. 6 The main parameters of the rabbit schematic eye in diagrammatic form. Measurements are given in mm. from the corneal vertex or between points indicated by arrows. The refractive index of the various media is indicated by a suffixed letter n.



RETINAL HISTOLOGY

INTRODUCTION

Retinal single unit analysis has shown the rabbit to be unusual amongst the studied mammals because of the variety and profusion of units with a sophisticated function (see p. 49). The rabbit retina has been neglected in the histological literature and a limited investigation was thus undertaken in order to see if its organisation is typical of the more commonly studied forms.

The early literature contains a few references to the giant ganglion cells of the rabbit retina (Dogiel, 1883; Schiefferdecker, 1886). Cajal (1893) illustrates a small clump of amacrine cells. More recently an investigation of the horizontal cells was undertaken by Dowling, Brown and Major (1966) and of the inner plexiform layer by Raviola and Raviola (1967). Sjöstrand (1964) has presented an EM survey of the rabbit retina which concentrates upon the receptor organisation. His description is confirmed by the present work.

The following section has been broken into two components. The problem of whether cones exist in the rabbit retina has been separated out from the general description of the retinal histology.

METHODS

The camera lucida drawings of receptors, horizontal cells, some amacrine and Muller cells were made from Golgi material prepared as described in the section on histological techniques included in the chapter on methods.

Drawings of other amacrine and ganglion cells both in radial section and squash mount are from material stained 'in vivo' with methylene blue (see p. 268 for details).

Electron microphotographs are of ultrathin sections of retina fixed in osmic acid, mounted in Araldite and counterstained with lead (see p. 269 for details). The rod outer segments in these sections were poorly preserved.

CONES /

CONES

Prince's "The Rabbit Eye in Research" contains an editorial apologetic for the presentation, in adjacent chapters, of both confirmation and denial of the existence of cones in the rabbit retina. The rod and cone are clearly defined entities in the primate retina examined under light microscopy. The attribution of a differentiated physiological function to each of these forms has led to the 'duplicity theory' in which it is stated that the rod is the organ of vision in dim (scotopic) light and the cone is the receptor for bright (photopic) light and colour vision. Since von Kries outlined the theory there has been an accretion of properties attributed to the cone so that the presence or absence of this morphological feature in the rabbit might imply, for many, a great deal more than is justifiable about the physiology of this animal's vision e.g. the high acuity of human cone vision is much more dependent upon the presence of a path to the C.N.S. which is of low convergence than upon the presence of the cone itself. The application of the electron microscope to the examination of receptor structure and the extension of the number of species investigated has led to considerable problems of nomenclature for those cases in which the assumed concomitants of cone vision become independent variables. Pedler (1965) has addressed some preliminary comments to this problem.

Electron microscope examination of ultrathin sections and light microscope examination of Golgi preparations was undertaken in order to determine whether 'typical' cones exist in the rabbit retina.

Results. Two types of outer-inner segment complex were observed in the electron microscopic examination of the retina. The great majority of the outer segments are typical rod types (Sjöstrand class I) possessing long, slender, cylindrical forms. The second type (class II) has a short outer segment, about $\frac{1}{2}$ to $\frac{1}{3}$ of the length of the rod type, which is surrounded at its vitread end by the large inner segment which pushes up between the rod outer segments. The scleral end of the type II receptor outer segment is wrapped around by processes coming from a pigment epithelial cell. In tangential section, the outer segment of the type II receptor may be seen as a lamellated /

lamellated structure amongst the rods.

The preceding description confirms the findings of Sjöstrand (1964) as do my observations on the receptor end feet at the outer plexiform layer. The most numerous end foot form (Sjöstrand α type) is ovoid and displays a single synaptic ribbon in association with two vacuoles if it is viewed in vertical section. The second type of receptor foot (β type) is triangular in vertical section and appears to contain numerous processes and synaptic ribbons.

Accurate estimates of the ratio of type I to type II receptors and of α to β end feet have not been made. Sjöstrand (1964) mentions an excess of β type end feet over type II receptors. A straightforward count revealed 60 type II receptors amongst 570 type I outer segments while 14 β type pedicles were counted amongst 154 α pedicles. The ratio of type I to type II receptors is thus 9.5:1 and of α to β end feet is 11:1.

A number of receptors have been stained in their entirety in the Golgi preparations, while remaining unobscured by adjacent cells, so that it was possible to follow the fibre from the inner segment to the foot. The most common type was the typical rod whose ovoid foot is clearly the same as the α foot found in the EM photographs.

The second form was very uncommon and in only three cases could a fibre be traced from the inner segment to the foot. None of these cells possessed a completely impregnated outer segment. The inner segment was rather fat and bulged into the rod outer segment region. The nuclei were adjacent to the outer limiting membrane and the pedicle was triangular in section and possessed a number of basal processes. The appearance of the pedicle was similar to that of the β type observed under the electron microscope.

Illustrations of the cells referred to in this section will be found (p29) on reference to the section dealing with the general histology of the retina.

Discussion

Does the rabbit possess 'typical' cones?

If the cone is regarded as a receptor with a conical outer segment then it is necessary /

necessary to agree with Sjöstrand (1964) and accept that the rabbit does not possess typical cones. The type II receptor found during EM examination of the retina is characteristic of the rabbit and unlike the cones of other species. The question thus becomes whether the type II receptor may be regarded as an atypical cone.

The completely impregnated rods of the Golgi preparation clearly possess an outer segment which corresponds with the type I receptor of the EM photographs and a foot, or spherule, which is similar to the α pedicle of the EM pictures.

The classic cone of a Golgi preparation may be recognised by features other than its outer segment shape. The inner segment is broad, the nucleus is close to the outer limiting membrane and is well clad in cytoplasm while the pedicle is broad, appearing triangular in vertical section, and gives off a number of slender processes. The pedicle is clearly of the EM β type. The three completely impregnated cells of the Golgi preparation which possessed the β type pedicle showed all of the above cone features. Although the outer segment was not completely impregnated in any of the cells it is clear from the description of the inner segment that this portion must correspond to the inner segment of the type II receptor.

Only the two types of receptor were observed in the Golgi preparations and these are classed as the I α and the II β forms. An examination of a number of EM photographs of the retina indicates that the I α type must be by far the most common. It would be wrong, however, to assume that only these two forms are present on the basis of the foregoing evidence. Kalberer and Pedler (1963) found the complex, β , pedicle to form 50% of the total in the alligator while only 1 in 10 of the receptors were cones. Nobody has yet attempted to trace the thin filaments from one type of pedicle to its outer segment in serial EM sections.* Stell (1966) has, however, performed an equivalent feat by the elegant technique of studying the same Golgi stained receptor by both light and electron microscopy. In the teleost retinas' studied it is apparent that the identification of the α and β pedicle with rod /

*See fig.10

rod and cone feet respectively is a safe procedure. The result of the count described in the previous section supports the extension of Stell's finding to the rabbit retina. The close agreement of the ratios type I/type II (9.5:1) and α/β (11:1) argues strongly for the presence of I α and II β receptors alone.

Apart from the unusual form of the outer segment, the type II β receptor is very similar to the classic cone. Two further points of correspondence may be mentioned. The cones of other species characteristically show numerous mitochondria in the distal portion of the inner segment while the discs of the outer segments do not possess the button like edges found in the rods (Boycott & Dowling, 1967); both of these features are found in the type II outer segments.

The subsequent sections will demonstrate that the rabbit visual system behaves in certain ways characteristic of species possessing the classic cone form. In view of the identity of the I α receptor with the rod and the absence of any receptor type other than the class II β form to which these functional properties may be attributed it will be convenient to refer to the II β type as cones. This title is, after all, not withheld from the atypical, non-conical, cones of the human fovea.

Scotopic and photopic mechanisms. Having established the presence of atypical cones in the rabbit retina we must now consider whether they are sufficiently numerous to contribute a separate photopic phase to the overall response of the eye.

Dodt and Elenius (1960) have determined the light energy required for a constant electroretinographic response to a flash of light during the process of dark adaptation. It was observed that the sensitivity curve showed a distinct kink beginning after 50 min. in the dark. The process of adaptation took 3 hours. The sensitivity of the E.R.G. to white light and to beams of max 462 and 605 m μ was the same at all times during dark adaptation. The curve is similar to that obtained from the human eye in which the first part is attributed to the cones and the second to rods. The results of testing with coloured beams suggests that the photopic and scotopic mechanisms have similar /

similar peak spectral sensitivities.

Only one pigment has so far been extracted from the rabbit outer segments and that is a typical vertebrate rhodopsin with a peak absorption at 502 m μ (Kbttgen & Abelsdorff, 1896; Wald, 1938; Bridges, 1959). The same peak was found in the in vivo bleaching experiments of Rushton et al. (1955). The guinea pig shows a photopic mechanism less well developed than that of the rabbit yet Weale (1955) found that the density changes caused by bleaching of the retina in blue light were by no means as extensive as the changes occurring in white light. It thus appears that other pigments may be present in the guinea pig photoreceptors. The experiment has not been performed on the rabbit but, as will be seen, it is likely that similar results would be obtained. A small population of receptors containing a pigment other than rhodopsin may be of physiological significance if located together and yet be undetectable by gross sampling techniques such as pigment extraction.

Elenius (1958) has used the flicker fusion frequency of the ERG b wave as an index of the dark adaptation properties of the rabbit eye. The flicker fusion threshold curve shows a kink at about 30 per second for an illumination intensity of 800 lux. The upper branch of the curve will follow flicker up to 75 per second at 8,000 lux. The two phase flicker fusion curve was described by Porter in 1902 and the first component, responding up to 30 cycles per second, was shown by von Kries (1903) to be the result of the rod response. The curve beyond this region is generated by the cone response.

The spectral sensitivity curve of the ERG b wave provides a sensitive means of testing for a change over of functioning pigment in the transition from scotopic to photopic vision. In the cat the peak spectral sensitivity shifts about 55 m μ towards the red during light adaptation. The result is similar to that obtained in psychophysical experiments on human beings and is thus referred to as a Purkinje shift. The rabbit does not show this change clearly.

Elenius /

Elenius (1956) found that the peak sensitivity varied somewhat between individual rabbits but the results agreed with Wirth (1953) and Dodt and Walther (1958) in that the curve of the dark adapted animal possesses a hump at 460 to 470 m μ and a peak between 490 and 500 m μ . Elenius found orange light to be more effective as an adapting light for abolishing the b wave than a scotopically equivalent blue light. The difference was small and corresponded to a Purkinje shift of only 10 m μ . Dodt and Walther were unable to detect any Purkinje shift in their flicker fusion experiments on rabbits although such a change was readily found in the cat.

The graph of flicker fusion frequency against light intensity which was determined for the rabbit by Elenius is similar in form to Dodt and Enroth's (1953) curve for the cat; the kink in the curves is found at about 20° and 44° cycles respectively. The photopic mechanisms thus appear to have a similar cone basis. The absence of the Purkinje shift in the rabbit means no more than the presence of rhodopsin as the predominant pigment in the photopic mechanism. The elements of this system should not be referred to as cone-like rods (Granit, 1947; 1962) for their physiology is that of a cone and not that of the rod whose typical pigment they bear. Similarly Granit is mistaken in describing the rabbit as an animal not in possession of photopic dominators simply because these units demonstrate the same spectral sensitivity as the scotopic dominator (1963).

Elenius made the further interesting observation that if the rabbit retina was subject to light intensities great enough to activate the cones then the ERG b wave took considerably longer to return in the dark. 8,000 lux adaptation abolished the b wave fully and recovery took 4 hours. At 90 minutes the rhodopsin has been completely regenerated but the b wave is only 20% of maximum. The results suggest that the cones are able to suppress rod function. This may be part of the system which ensures that the limited number of cones available in the rabbit eye are able to dominate in the visual input to the brain under photopic conditions. The pupil control of the rabbit is not as well developed as is common amongst rod eyes and the above /

above phenomena may be an adaptation to the animal's arrhythmic behaviour.

Wavelength discrimination. Monnier et al. (1962) observed that the spectral sensitivity curve of the rabbit retina showed a slight hump at 450-480 m μ after light adaptation. Using averaging techniques, Monnier et al. (1963) found humps at 450 and at 530 m μ which were not present in the dark adaptation curve. Dødt and Elenius (1955) describe a widening of the peak of the single unit sensitivity curve in the blue during light adaptation. Later, Dødt (1956), excitatory and inhibitory effects on ganglion cell activity were described which showed marked, narrow peaks at 460, 520 and 560 m μ when the intensity was great enough to stimulate cones.

In the LGN, Hill (1962) describes units possessing a number of sensitivity peaks at 435, 445, 460, 505, 515, 580 and 635 m μ . Some possessed a broad band and others a narrow band response. At the cortical level, Monnier et al. (1963) describe increased sensitivity at 450 and 530 m μ in the electrocorticogram of light adapted animals when compared to the dark adapted preparation. At no level in the rabbit visual system is an unequivocal peak sensitivity present in the red. Such peaks as occur in albino rabbits appear to result from reflection of light from the choroidal blood vessels.

It would appear that an elementary mechanism for colour discrimination is available to the rabbit but the manner in which it is used remains a matter of some confusion.

Rabbit colour vision. Rabbits can be trained to respond to visual cues but neither Washburn and Abbot (1912) nor Watson and Watson (1913) were able to train the animal to distinguish between two equally bright coloured papers.

In view of the more recently accumulated electrophysiological evidence for wavelength discrimination, Nubser (1965) has attempted to reinvestigate the problem. In one paper he demonstrated that the optokinetic response shows two maxima of sensitivity; one when alternate stripes on the stimulating apparatus were of wavelength 480-490 m μ and the other when they were 510-520 m μ . These results (1965 a) are suggestive of a response in the rabbit which does not follow the simple rhodopsin sensitivity curve which has one peak.

A later report (1965 b) indicated that the rabbit is capable of discriminating all grey filters from a green filter ($P = 0.001$). It thus appears that the animal is able to use the colour discrimination available in the CNS for effective colour vision.

Summary. The foregoing discussion may appear inordinately long in comparison with the length of the results section which preceded it. The review was included to show that, in spite of statements to the contrary in the literature, there is strong evidence for

- (1) The presence of cones in the rabbit retina.
- (2) The presence of separate scotopic and photopic mechanisms the latter of which shows features of a cone based system.
- (3) Wavelength discrimination at various levels in the CNS.
- (4) Effective colour vision.

GENERAL HISTOLOGY OF RABBIT RETINA

The previous section was specifically directed towards the establishment of the presence of cones amongst the receptors of the rabbit retina. The following section examines the general retinal histology of the same animal.

Results.

Pigment cells.

In fig. 7, which is a composite drawing of the various retinal cell types found in Golgi and methylene blue preparations, the pigment cells are shown with a protruding nucleus as they appear in Golgi preparations. Photographs of retina which has not undergone impregnation show the cells as flat and elongated in sagittal section. In tangential section the cells are polygonal and have a central nucleus. The pigment granules lie within the cytoplasm of the cells and are readily identified under the EM (fig. 8).

Receptors.

The appearance of the receptors in Golgi preparations is shown in fig. 7c (rods) and 7d (cones). As previously described, the cone outer segments end in the pigment cells and may be seen in section to be surrounded by pigment cell /

cell processes which sometimes extend half way down the outer segment (fig. 9). The cone inner segment extends well beyond those of the rods into the region of the rod outer segments. This may be seen in sagittal section in fig. 10 and in transverse section in fig. 11. At the level of the inner segments it is often possible in, transverse section, to see the 'cilium' which joins the inner to the outer segment in both rods and cones. In fig. 12 the section is taken at the level of the rod mitochondria. The section is almost at the level of the outer segments, as may be seen by the patches of broken down plaque, and a number of cross sections of the cilium are visible; each is recognisable by the nine dark spots around its periphery that represent sections through the filaments which run along its length. The cone outer segments are much longer than those of the rod and contain mitochondria only at their scleral end. They are thus readily identifiable in more vitread tangential sections (fig. 13) on which level their Golgi apparatus is located.

Rod pedicles predominate amongst the nuclei of the vitreal portion of the outer nuclear layer and at the scleral edge of the outer plexiform layer. The cone pedicles are situated more deeply in the outer plexiform layer. Variation in the appearance of the rods in the Golgi material is confined to the position of the nuclei on the rod fibre. A number of rods may be seen which bear the nucleus adjacent to the outer plexiform layer while the rod spherule sprouts from the nucleus itself (fig. 7c). Such juxta-plexiform nuclei are readily identified in EM sections (compare fig. 7c with EM picture fig. 14). The difference between the rod and cone pedicles in sagittal section may be seen in fig. 15 which shows the whole width of the outer plexiform layer from the bipolar nuclei to the receptor nuclei. Another rod foot is shown in fig. 16. The bipolar processes may be seen to penetrate to the single synaptic ribbon. A darkly staining region, which may be the contact point of a cone process, can be seen on the surface of the spherule. The complexity of the cone foot with its multiplicity of processes is seen in tangential section in fig. 17. Fig. 18 shows a similar cone cross section /

section and is included, in spite of microtome chatter, to show the roots of the cone processes which may also be seen stemming from the pedicle of the Golgi stained cones (fig. 7d) (fig. 10).

Muller Cells.

In Golgi preparations it is possible to observe the Muller cells as apparently extending across nearly the whole width of the retina (fig. 76). The Muller fibres are readily visible in a very lightly stained preparation of the rabbit retina in which they are exceedingly well represented (they were discovered in the hare). The light microphotographs of figs. 36 show the fibres as beginning at the inner limiting membrane in the form of an expanded foot leading to a trunk which passes to the outer limiting membrane. The cell bodies are somewhat triangular in shape and are located in the layer of bipolar nuclei. The Golgi sections show that the Muller cells give off processes which pass for considerable distance along the inner and outer plexiform layers and rather shorter tendrils which form a network around the bipolar and receptor nuclei.

The Muller cell of the Golgi preparation appears to broaden at the level of the outer limiting membrane and gives off a number of short processes which penetrate between the inner segments of the receptors. The external limiting membrane appears, in these sections, to be formed from the expansions of the Muller cells. The Muller cell 'microvilli' are clearly shown in the EM photographs as packing the space between the inner segments (compare the drawing of fig. 76 with fig. 19). More vitread tangential sections reveal the junction of these processes to form the expansion of the Muller cell at the level of the 'outer limiting membrane'. The expansion may be seen to surround several outer segments (fig. 20) but is separated from them by a small space bordering which the Muller cell and receptor membranes may be clearly seen. The denser cytoplasm of the attachment zone between the Muller cell and the inner segments may be seen at this border in some regions of the photograph. Below the level of the attachment zones the receptor nuclei appear. Tangential sections show the receptor fibres, nuclei and Muller cell processes in a complex tangle (fig. 22).

Horizontal Cells.

Two types of horizontal cell were observed. One form lay in the innermost portion of the outer plexiform layer and possesses a flattened nucleus (fig. 7e). The other type of cell possessed a rounded nucleus located well within the inner nuclear layer (fig. 7f).

Bipolar Cells.

The bipolar cells were also found to form two classes. One type bore a fairly restricted clump of short processes, in the outer plexiform layer, which passed up to the receptor pedicles. The axon of this cell type passed straight down to the region of the ganglion cell bodies and there gave rise to a small number of terminal expansions (fig. 7g). The other class of bipolar cell spread out more widely in the outer plexiform layer before connecting to the receptors and possessed a vitreal process which arborised within a limited stratum of the inner plexiform layer (fig. 7h).

Amacrine Cells.

The Golgi material contained a few amacrine cells which all lay in the most vitread layer of the inner nuclear layer. The branches were either stratified (fig. 7i) or spread through a number of laminae of the inner plexiform layer (fig. 7j). In the methylene blue squash mounts these cells were numerous and readily identifiable by their position, size and absence of axon. Figure 23 shows a collection of the cells. One form possesses a relatively circular dendritic tree which is quite dense and consists of processes which appear flattened and, at the base, quite thick (fig. 23a). Another class possessed a bipolar form and a sparse dendritic tree which extended for over 300 μ along its major axis (23b). The more compact amacrine fields were about 100 μ in diameter.

Ganglion Cells.

The ganglion cells of the rabbit show an enormous variety of shape and size. Cells with from one to seven dendritic stalks branching out from the perikaryon have been observed in plenty. The broad stalks penetrate to a certain level of the inner plexiform layer and then give rise to profuse branches /

branches which may spread, in the case of the larger cells, for up to two millimetres. The cells of fig. 24 have been chosen to illustrate the various common types and are not a random collection. No cells with the multi-layered stratification were observed. No attempt was made to classify the cell types or their distribution.

Figure 25 shows a collection of ganglion cells from the region of retina below the optic nerve head. Some of the dendritic trees show a more or less circular distribution (fig. 25a) but the majority are markedly oval. The ratio of the major to the minor axis averages about 2:1 for the group shown. In this region of the retina the long axis of the dendritic trees is arranged parallel to the long axis of the visual streak and at right angles to the incoming axon. The long axis of the dendritic field in other regions of the retina is found to be set, in almost all cases, at right angles to the incoming axon so that the dendritic trees at the end of the band of myelinated fibres are set with the long axis vertical as is shown in the inset of fig. 25.

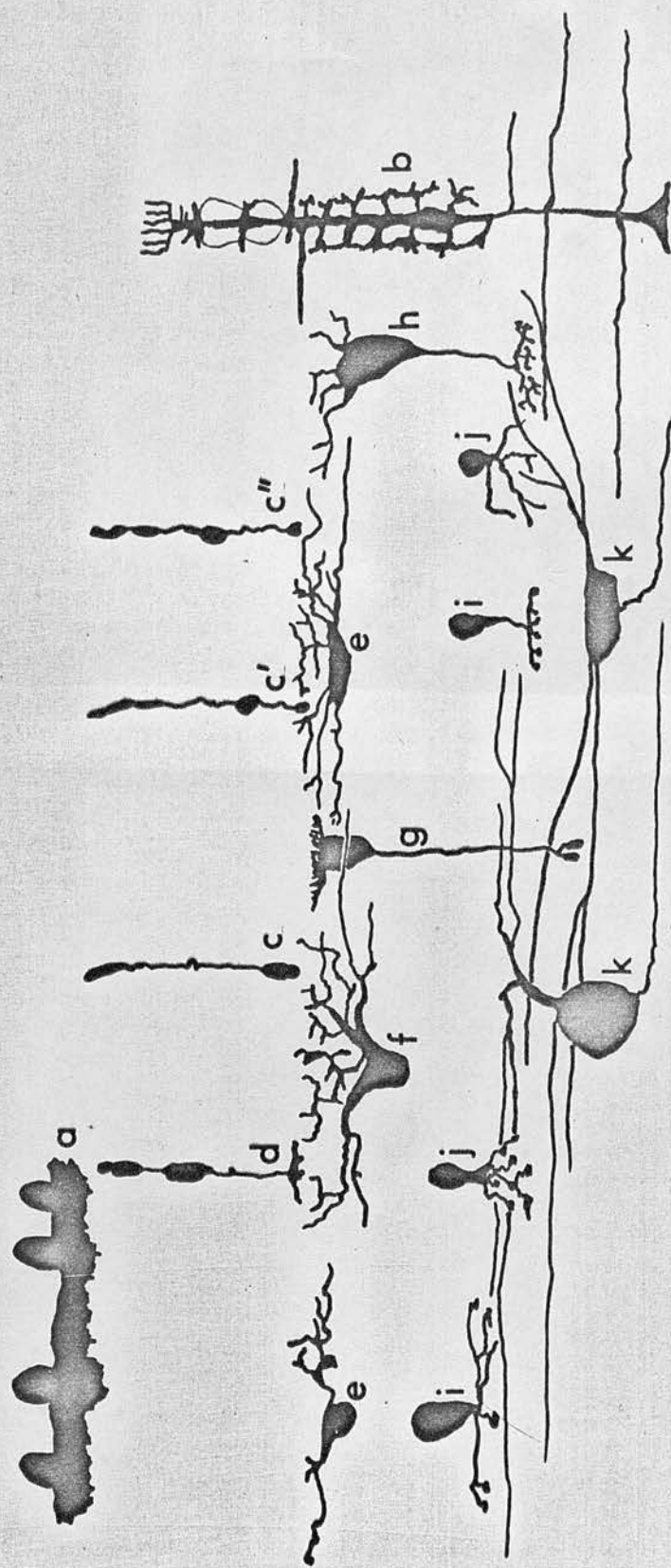
Discussion. Pedler (1961) has claimed that the outer limiting membrane and the Muller cell fibres stain differently, the former as collagen and the latter as neuroglia, and are separate structures. Sjöstrand (1949) has pointed out that the outer limiting membrane appears to be present at the level at which the rod outer segments change into rod fibres. It is in this region, he observed, that the whole circumference of the outer segments is seen to be organised as an attachment zone with the Muller fibre processes which surround them completely. It is Sjöstrand's contention that the outer limiting membrane is an artifact resulting from the differential staining of the attachment zones. My own findings confirm the results of Sjöstrand (1949; 1964). The continuity of the microvilli with the Muller cell expansions and Muller cell fibres containing swollen mitochondria is readily established by examination of serial tangential sections. The appearance correlates well with the vertical sections presented by Sjöstrand.

The two classes of horizontal cell are similar to those described by Cajal /

Cajal (1911) as typical for the mammalian retina. Dowling et al. (1966) have examined the two types in squash mounts of Golgi material. The cells of the outer plexiform layer were found to have fields about 100-200 μ in diameter while those lying deeper are about 300-500 μ in diameter. One long process may run for some distance from the cell and then expand into a clump of large processes. Synaptic contacts with both bipolar soma and dendrites were observed while fine processes passed up to the receptor pedicles. Contacts with both bipolar and receptors were to be found on one process of the cells.

The bipolar cells and amacrine cells observed in Golgi preparations were similar to those described by Raviola and Raviola (1967). It seems unwise, however, to describe the bipolars with either Cajal's or Polyak's nomenclature until the actual relationship of the two types to the receptors has been ascertained.

Fig. 7 Composite drawing of retinal cellular elements from methylene blue and Golgi sections. a, pigment cells; b, Müller cell; c, rods; d, cones; e, f, horizontal cells; g, h, bipolar cells; i, j, amacrine cells; k, ganglion cells.



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Fig. 8 Pigment cell granules as seen under E.M. at a magnification of
30,000. Tangential section.

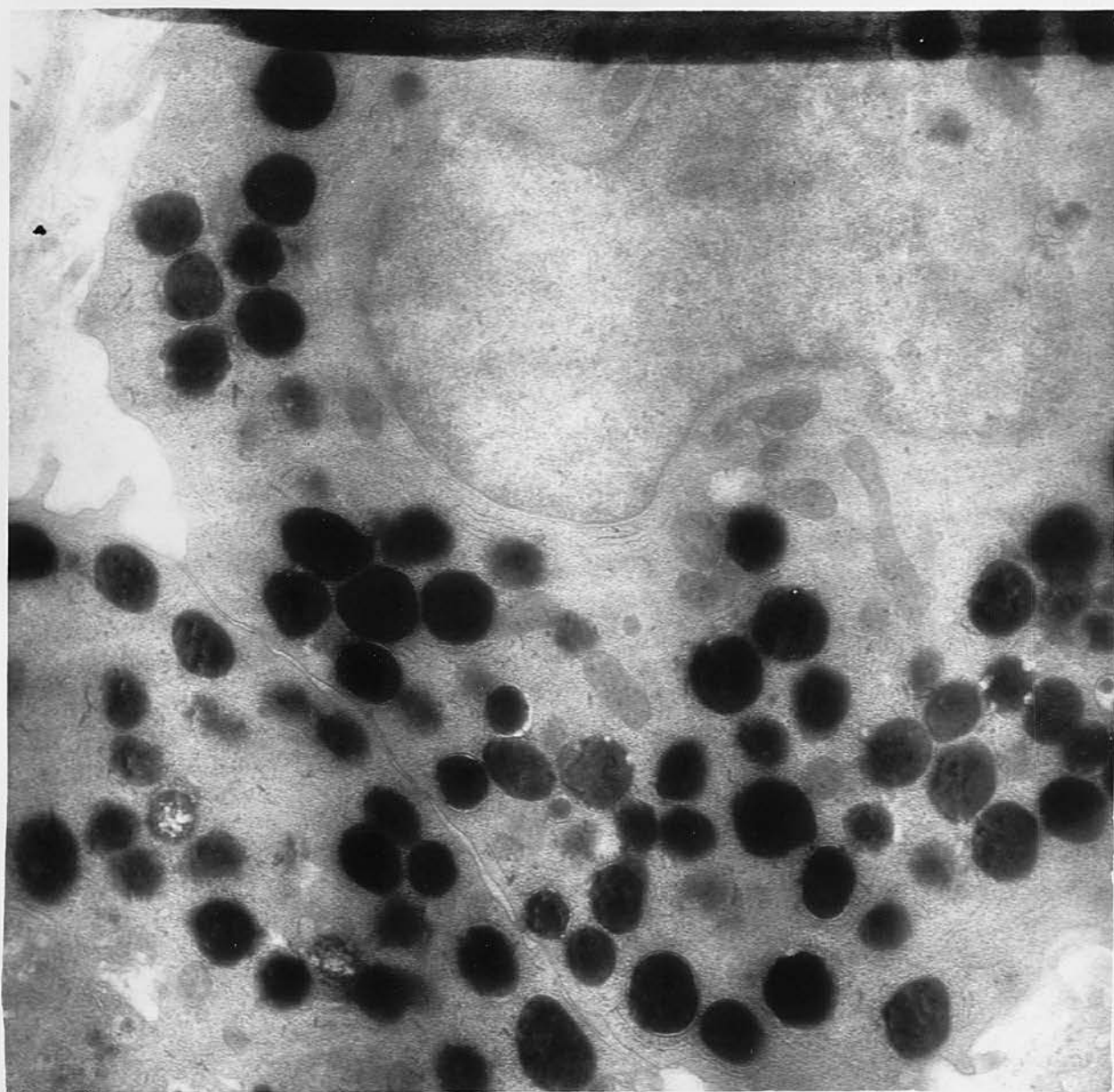


Fig. 9 Cone outer segment terminating in a pigment cell (pigment cell granules are visible and the cell nucleus is on the right margin) surrounded by lamellated processes from the pigment cell. Tangential section; E.M. at 30,000.

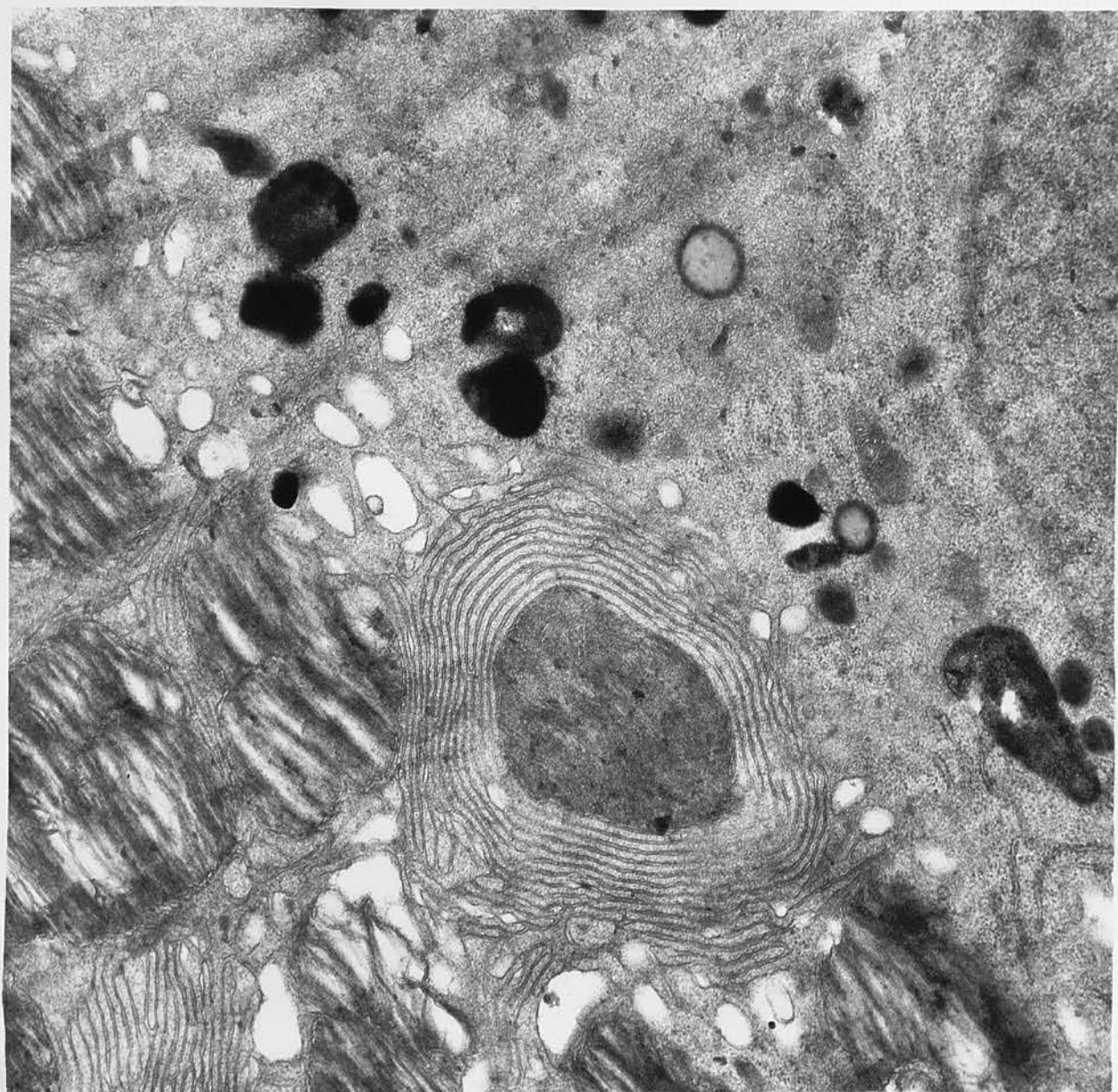


Fig. 10 A remarkable photograph showing the whole length of a radially sectioned rabbit atypical cone. Radial section; E.M. at 3,300.

At a may be seen the cone outer segment surrounded by pigment cell processes. At b is the cone inner segment containing mitochondria and protruding more sclerally than the rod inner segments. A more vitread region of the cone inner segment is shown at c which marks the region containing the Golgi apparatus. d is the cone nucleus, typically situated at the scleral boundary of the outer nuclear layer. Müller cell processes are present, e, and the arrows mark the fine branches which penetrate between the inner segments and are shown in cross section in fig. 19. f is the teledendron which terminates in the extended cone foot g; a small process typical of the cone foot passes out to the left. The actual junction between the filament f and the pedicle is very fine but was photographed in an adjacent section. In the adjacent serial sections the foot is seen to contain the more complex multiple synaptic bars characteristic of cone pedicles.

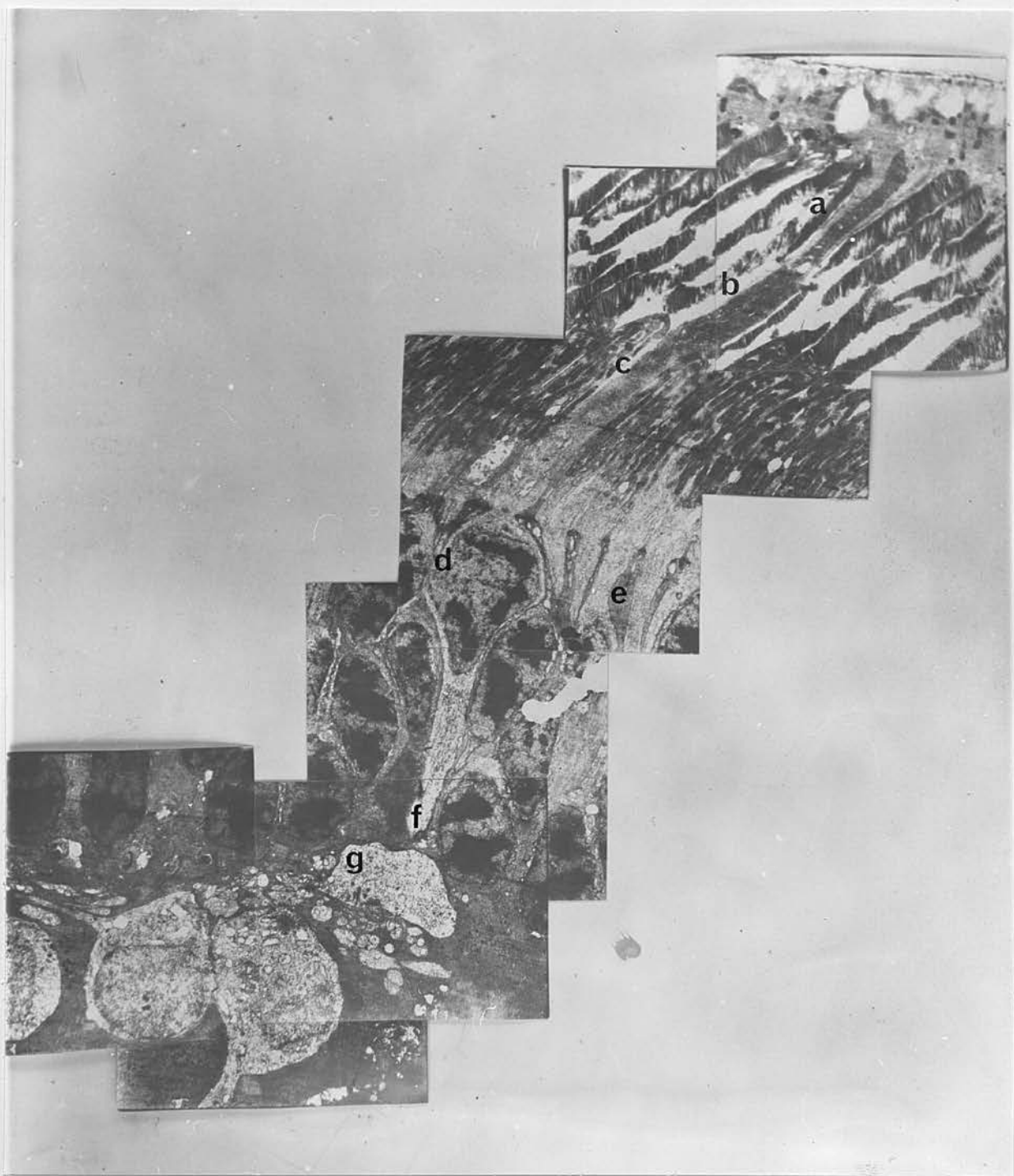


Fig. 11 The quality of this plate is poor but it shows a cross section of a cone inner segment in a plane scleral of the rod outer segments. The dark blur at the top right of the inner segment section represents the filament which connects the inner to the outer segment. The inner segment contains numerous mitochondria. E.M. 50,000.

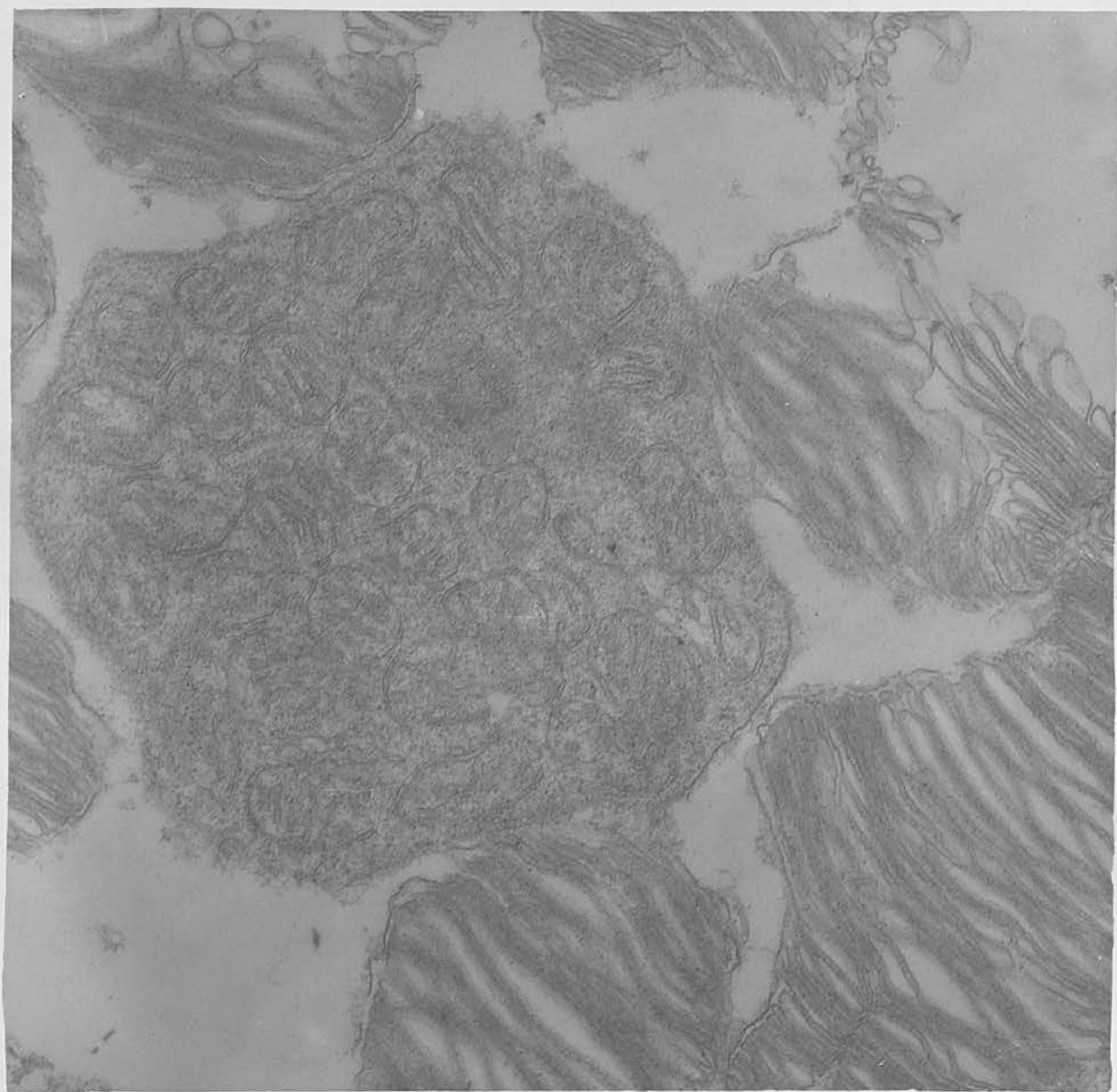


Fig. 12 A tangential section at the level of the mitochondria bearing region of the rod inner segments. The arrow heads indicate cross sections of cones whose inner segments contain the Golgi apparatus at this level. The complete arrows indicate sections through the filament which connects the inner and outer receptor segments. Close examination reveals the presence of nine sectioned processes around its circumference. E.M. 15,000.

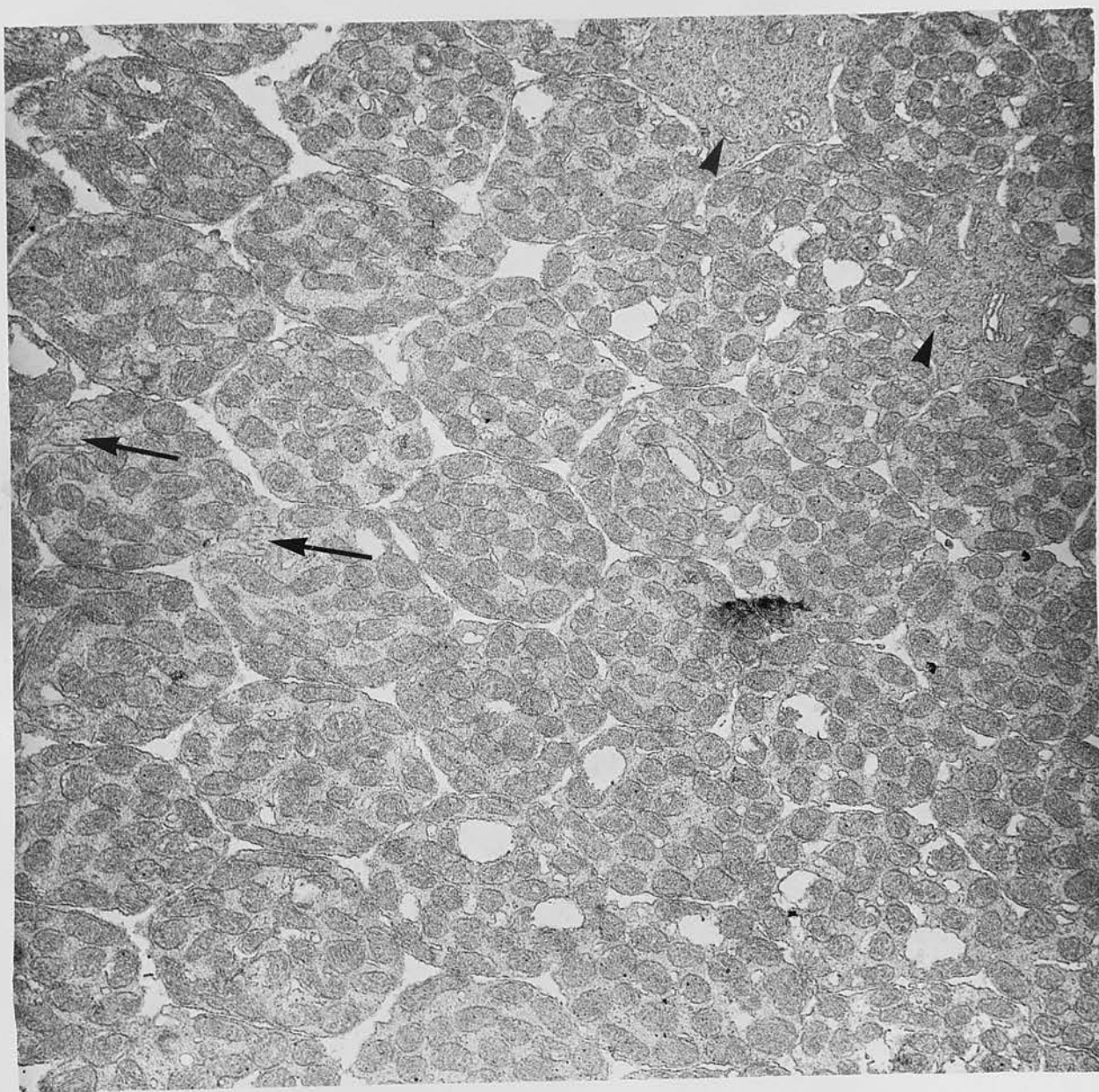


Fig. 13 A tangential section through a cone at the level of its Golgi apparatus. E.M. 40,000.

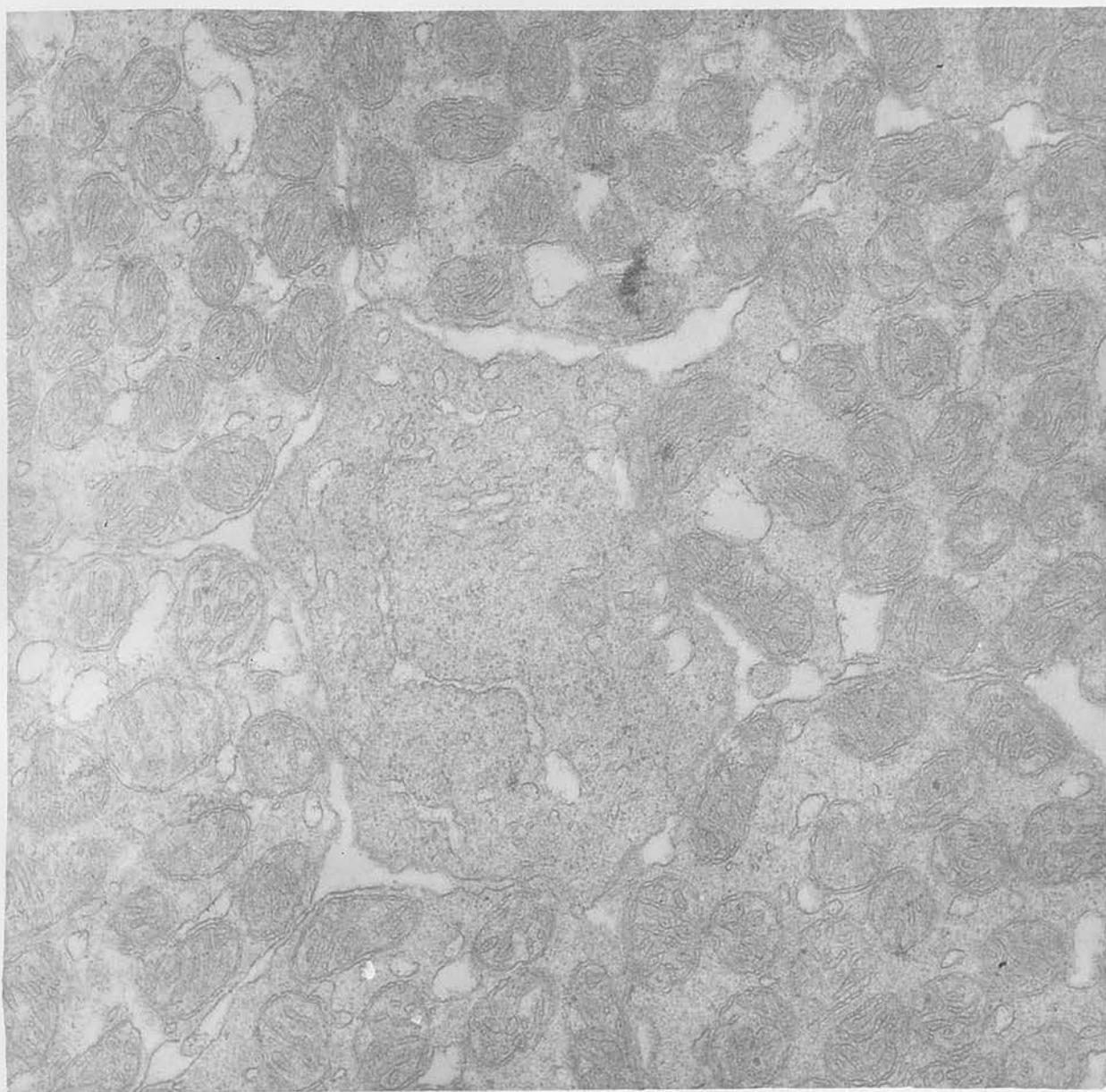


Fig. 14. Juxtaplexiform rod nucleus showing the spherule or rod pedicle, with synaptic bar and vesicles, sprouting from the nucleus. The appearance of such a nucleus under the light microscope is shown in fig. 7C. E.M. at 20,000.

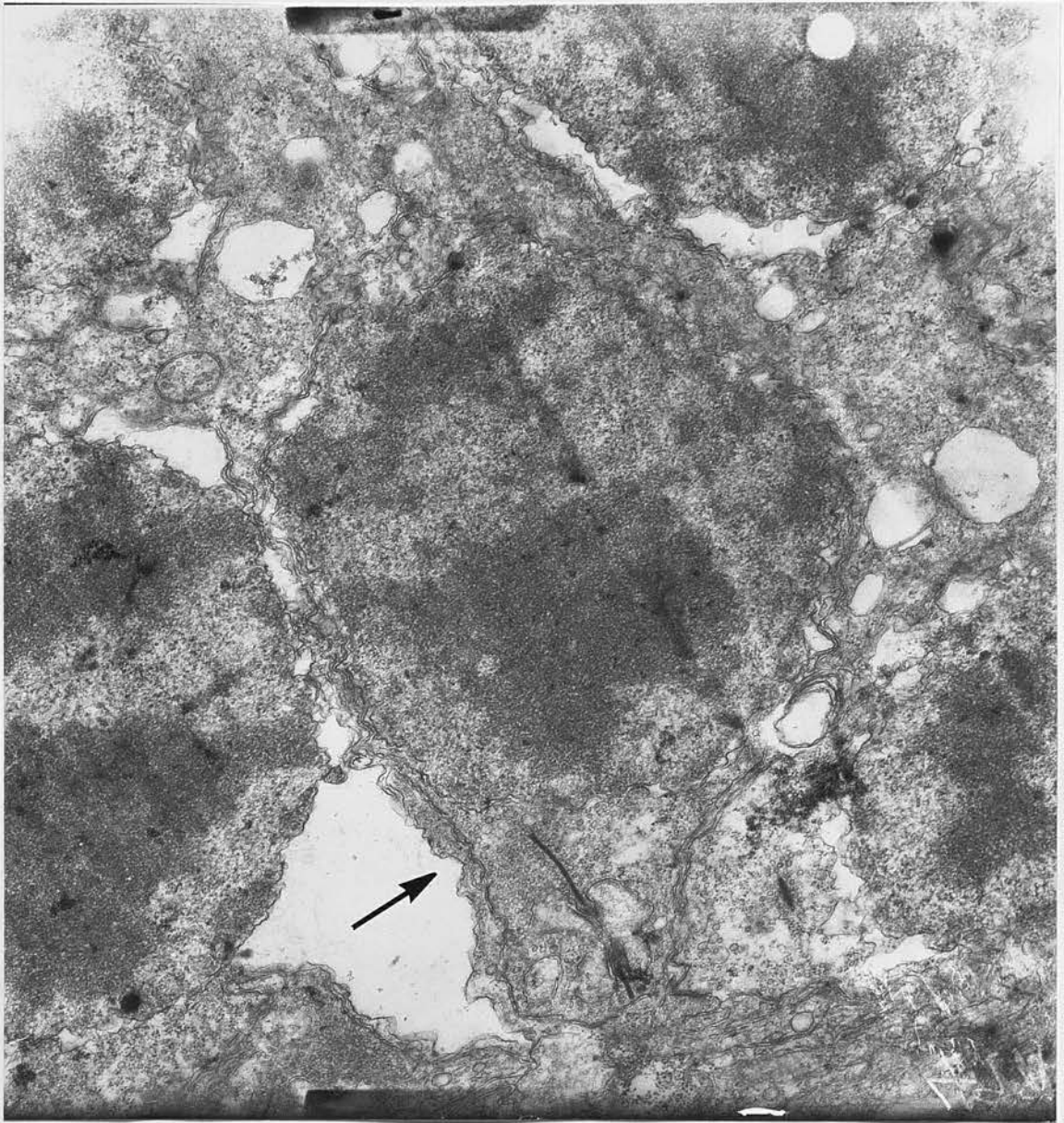


Fig. 15 Radial section through the outer plexiform layer. On the scleral side is a cone foot, C, with its characteristic triangular section. A number of closely packed processes enter the foot at the plexiform margin. R is a rod spherule with synaptic bar. The bipolar nuclei are visible on the vitread side of the picture, B. E.M. at 15,000.

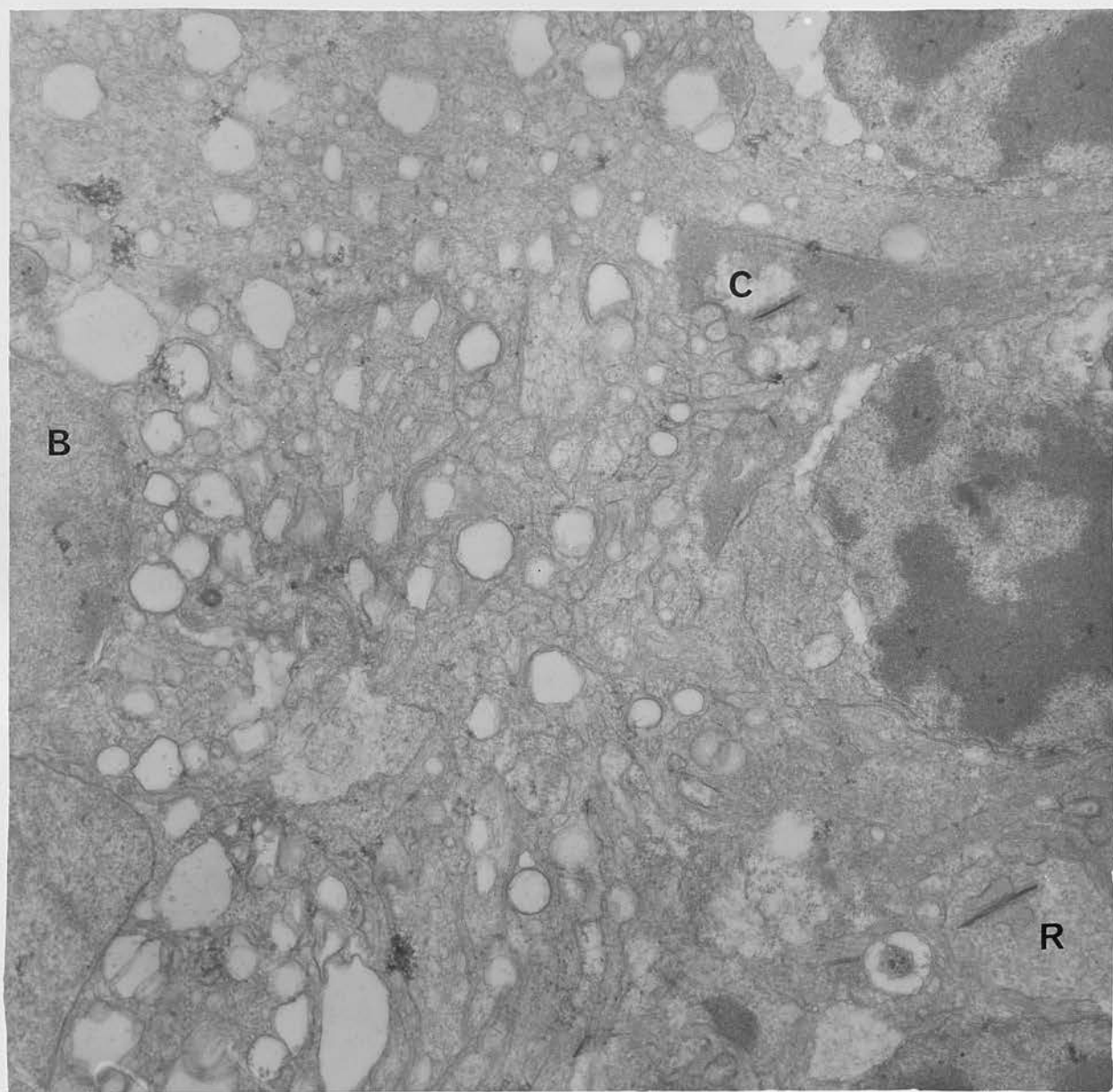


Fig. 16 High magnification (60,000) view of a rod spherule showing processes, perhaps bipolar dendrites, entering the foot (R). The synaptic bar is apparent. A darkly staining region on the lower left margin of the spherule may be the contact point of a cone process.

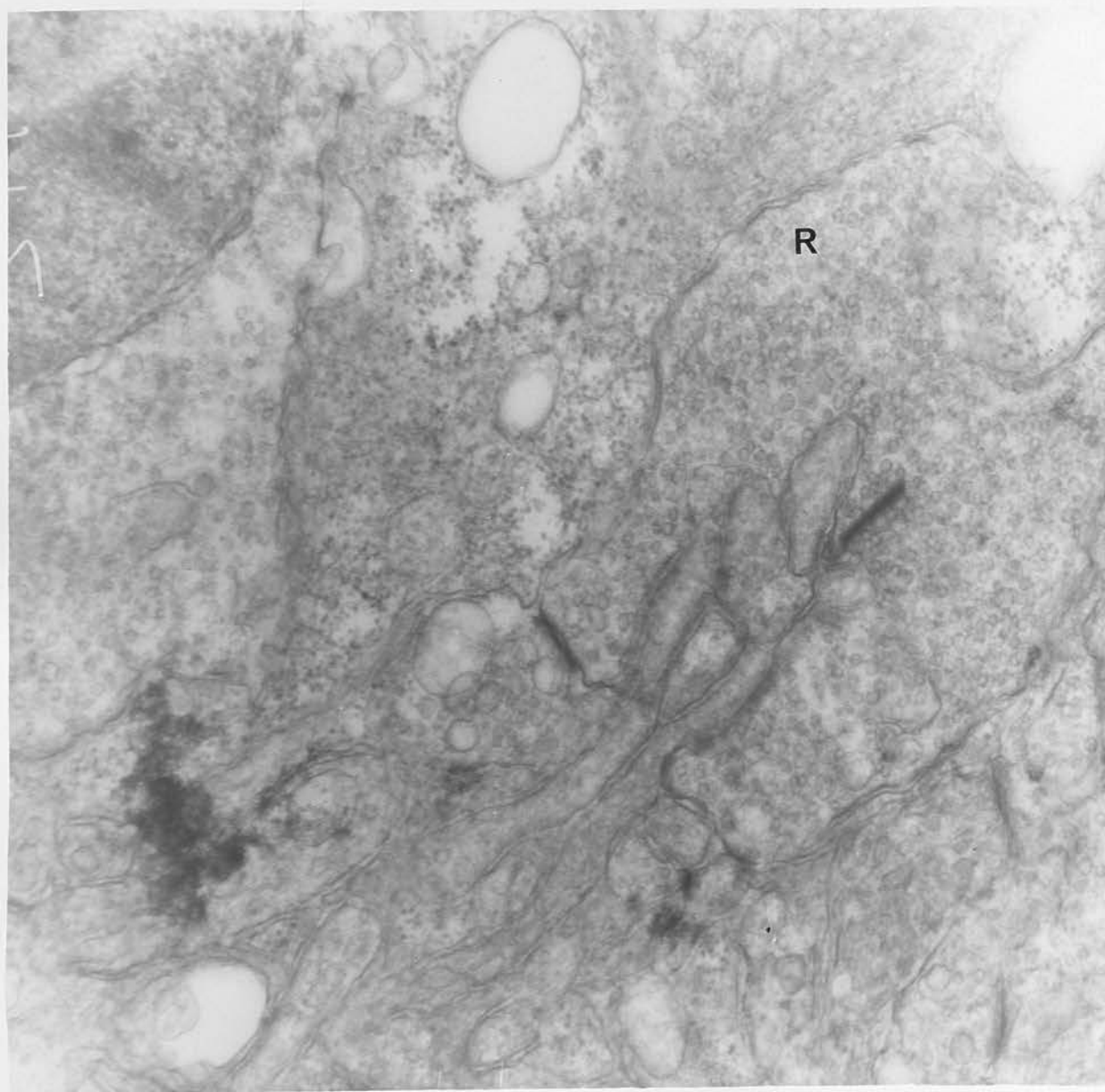


Fig. 17 A horizontal section through a cone foot at a magnification of 30,000 showing the complexity of this organ with its numerous synaptic bars.



Fig. 18 This is a similar photograph to the above but is included, in spite of microtome chatter, to show the processes which originate from the periphery of the cone foot. These processes are to be seen in fig. 10 and in the light microscope picture of fig. 7D. E.M. at 30,000.

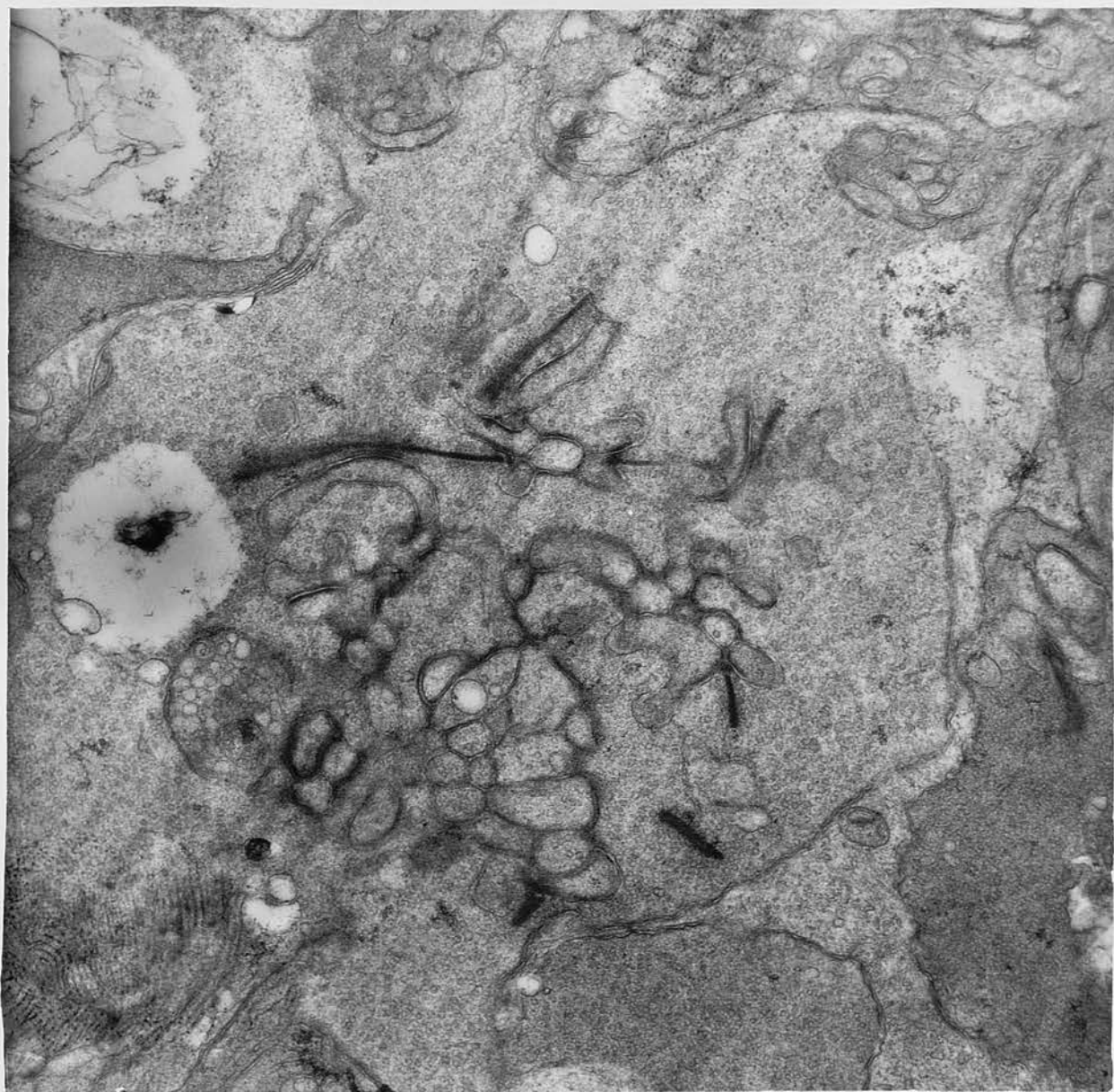


Fig. 19 Müller cell 'microvilli', V, packing space between rod inner segments. These processes may be seen at the arrow in fig. 10 and in the light microscope picture, 7B. E.M. at 40,000.

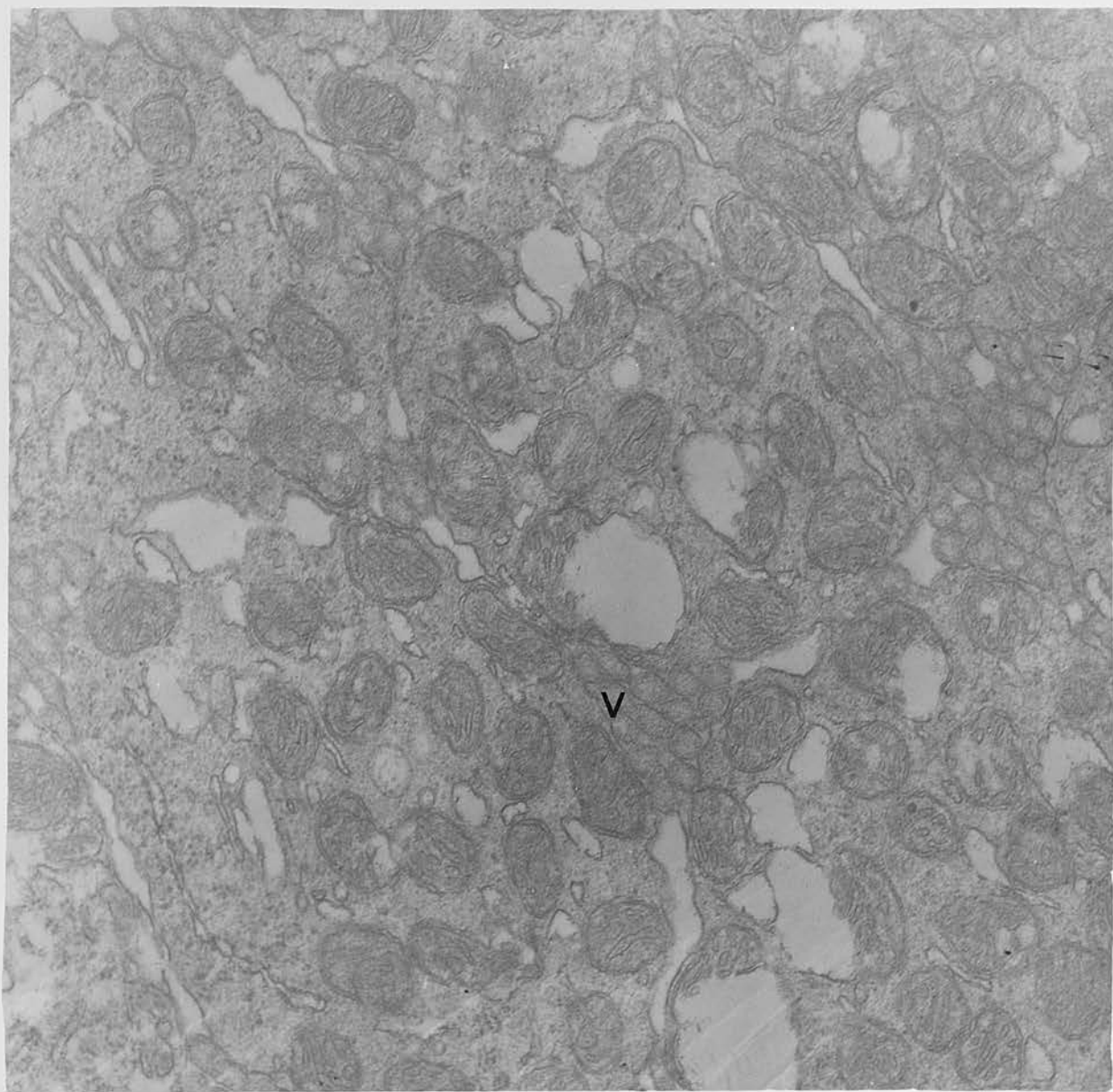


Fig. 20 Tangential section more vitread than fig. 19 showing rod inner segments, at the Golgi apparatus level, surrounded by Müller cells and revealing the expansion of the latter cells from which the microvilli sprout. The expansion surrounds several inner segments but is separated from them by a small space bordering which the cytoplasm stains darkly indicating an attachment zone. E.M. at 40,000.



Fig. 21 Angled tangential section somewhat more vitread than the previous one. The Müller cell in the lower part of the picture contains numerous partially disintegrated mitochondria. E.M. at 20,000.

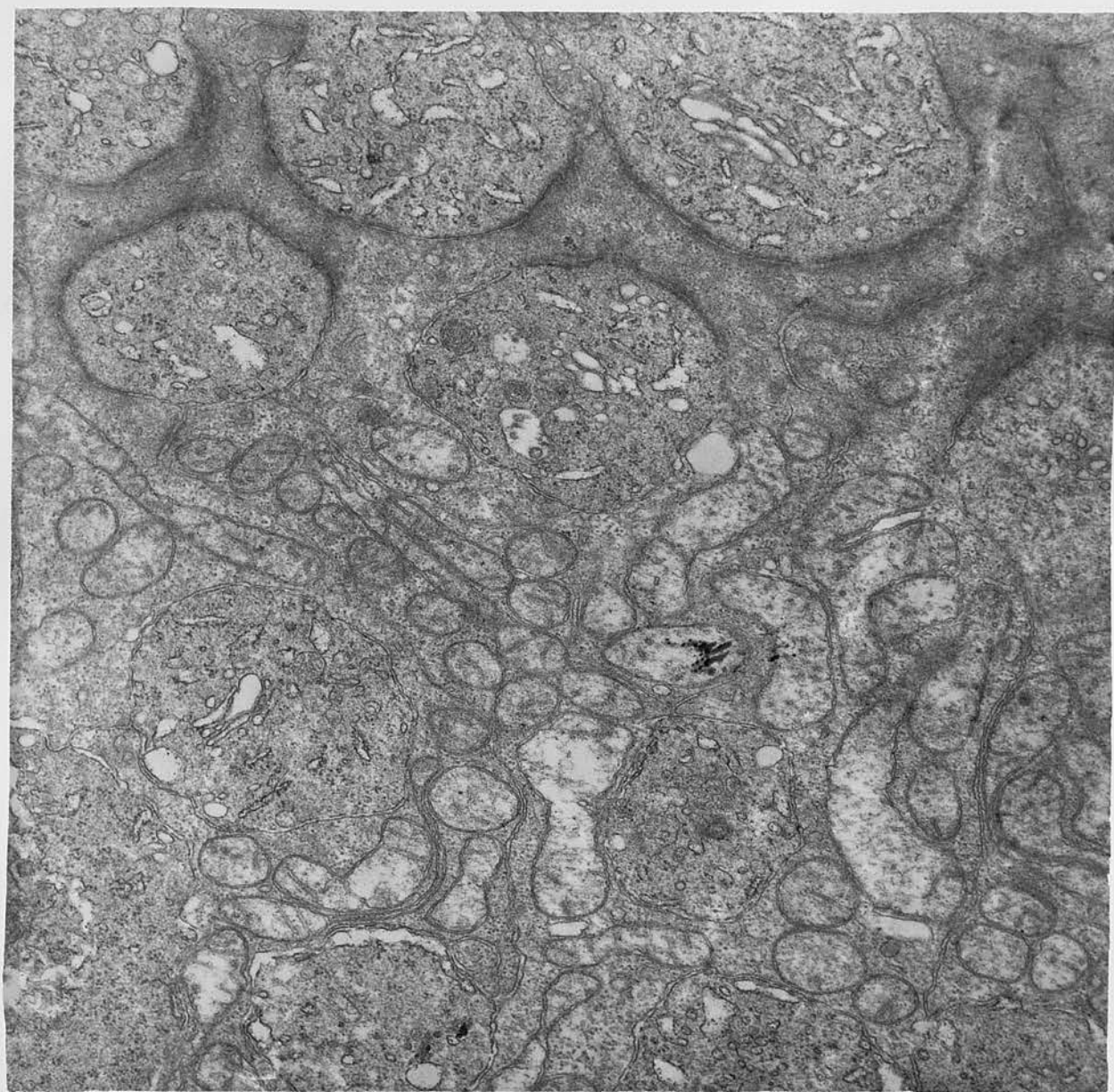


Fig. 22 Deeper tangential section, similar to the previous one, showing the beginning of the receptor nuclei amongst the inner segment and Müller cell processes.

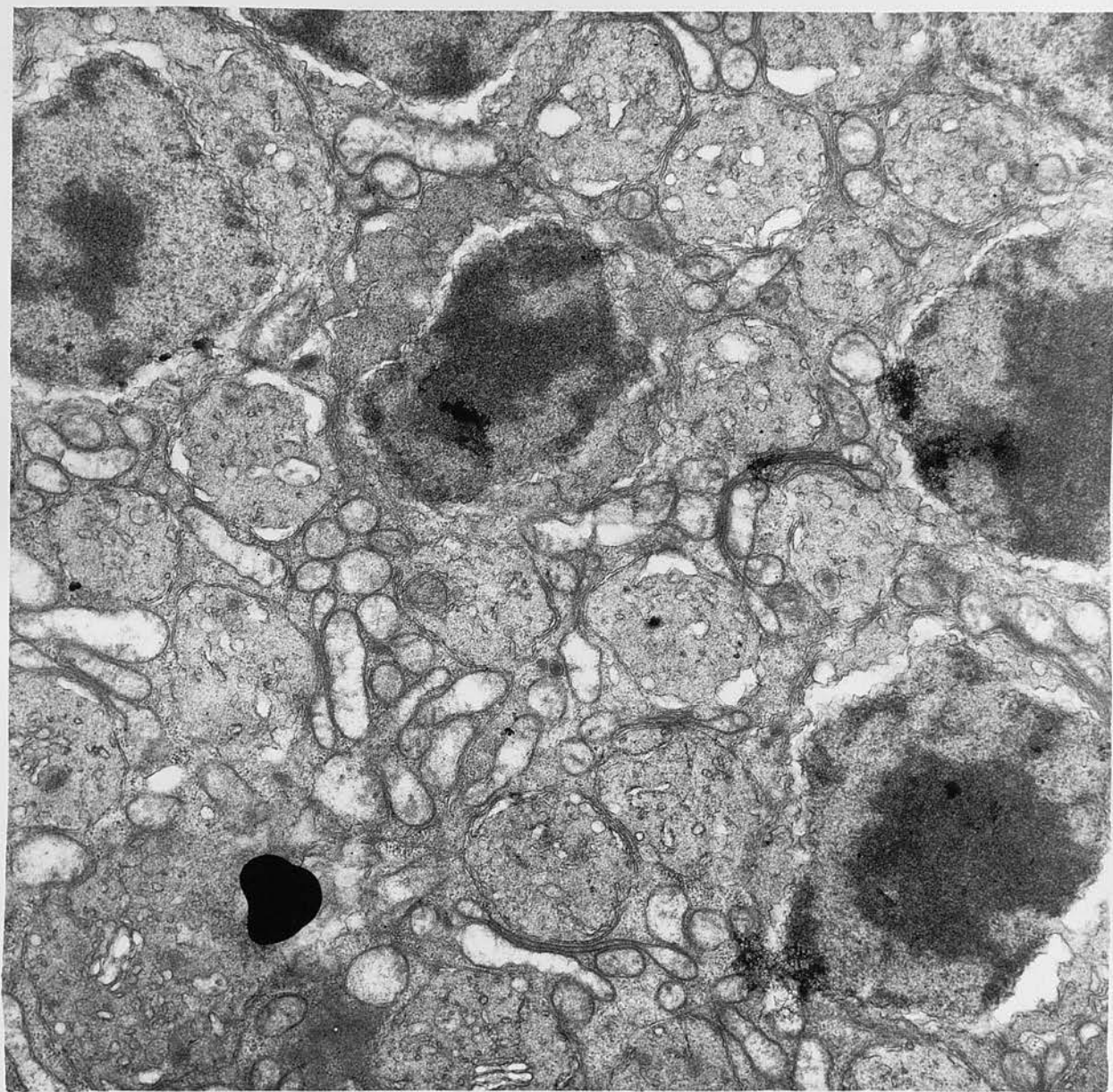
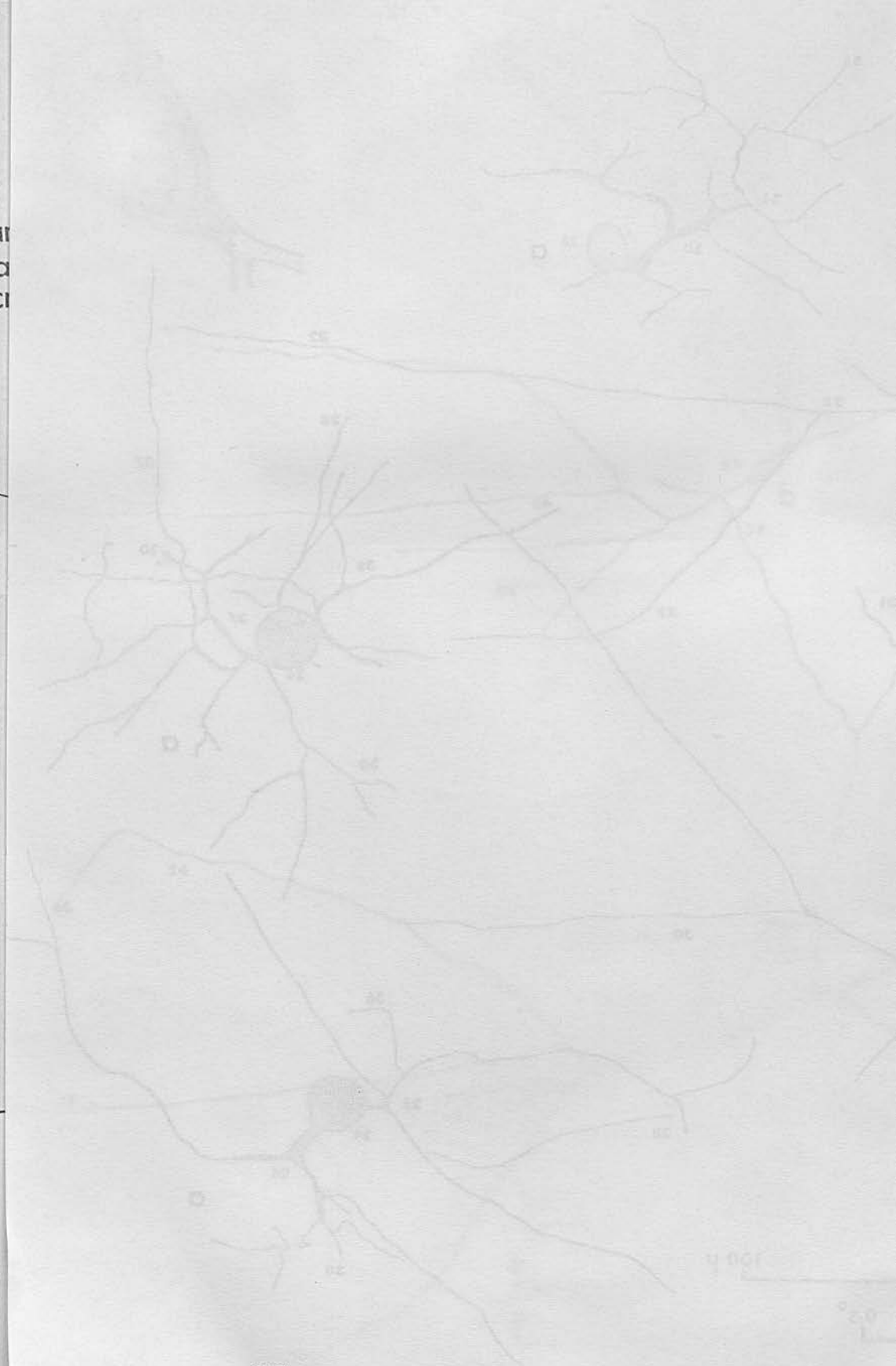
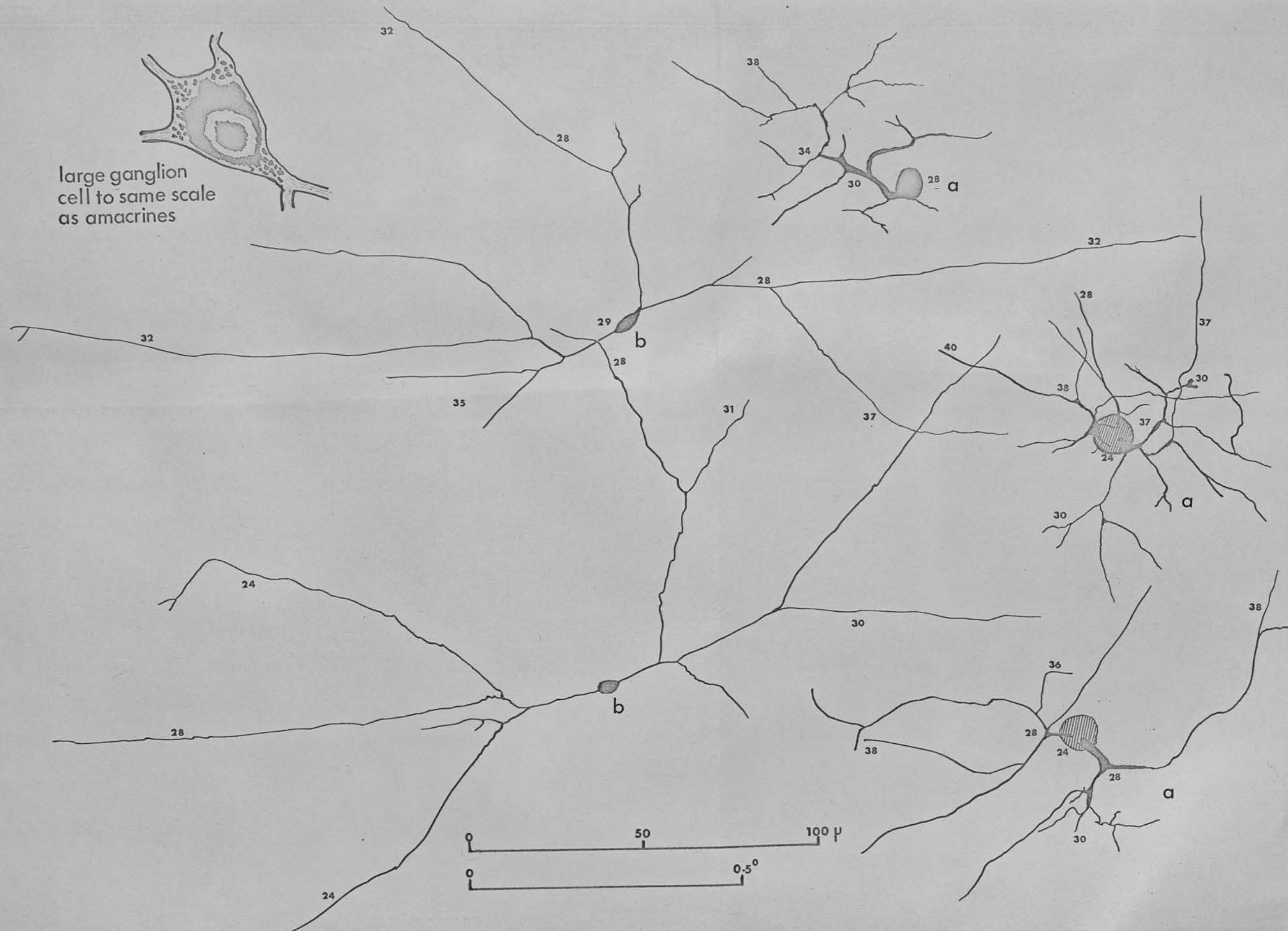


Fig. 23 Amacrine cells. a types have a dense circular or oval dendritic tree distribution which shows branching at various levels in the inner plexiform layer. b type is of bipolar dendritic tree form, more extended in distribution, and is restricted to one level of the plexiform layer in its branching. The numbers indicate depth of the adjacent process.

large gar
cell to sa
as amaci



large ganglion
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Fig. 24 Ganglion cells showing 1 to 6 basal dendrites drawn from 'in vivo' methylene blue squash mounts.



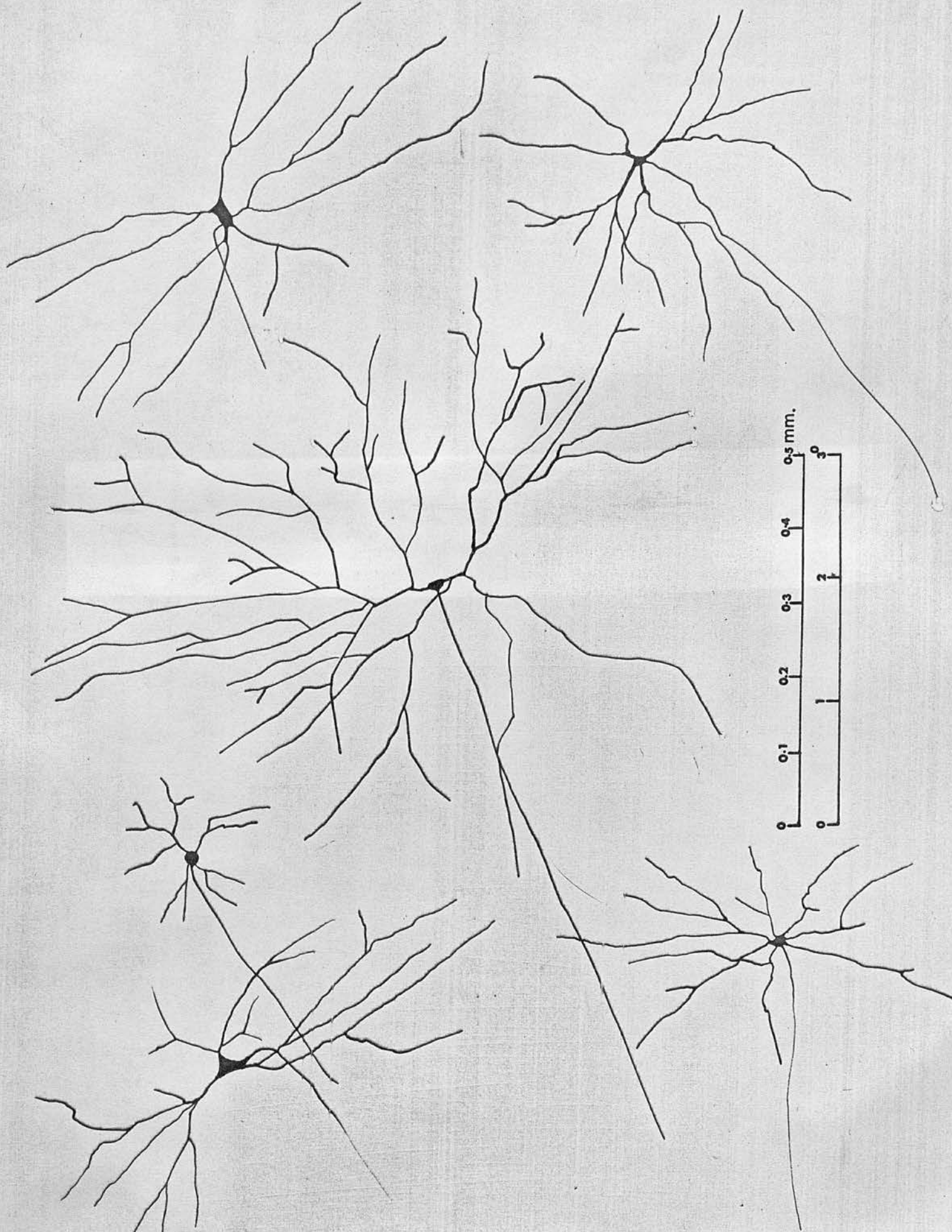


Fig. 25 Ganglion cells from the region of retina below the optic nerve head. Drawn from 'in vivo' methylene blue squash mounts. a is an example of the more rare circular dendritic tree distribution. The remainder are possessed of the common oval dendritic tree. Inset A shows an amacrine cell at the same scale. Inset B indicates the distribution of the dendritic tree major axis in different parts of the retina.

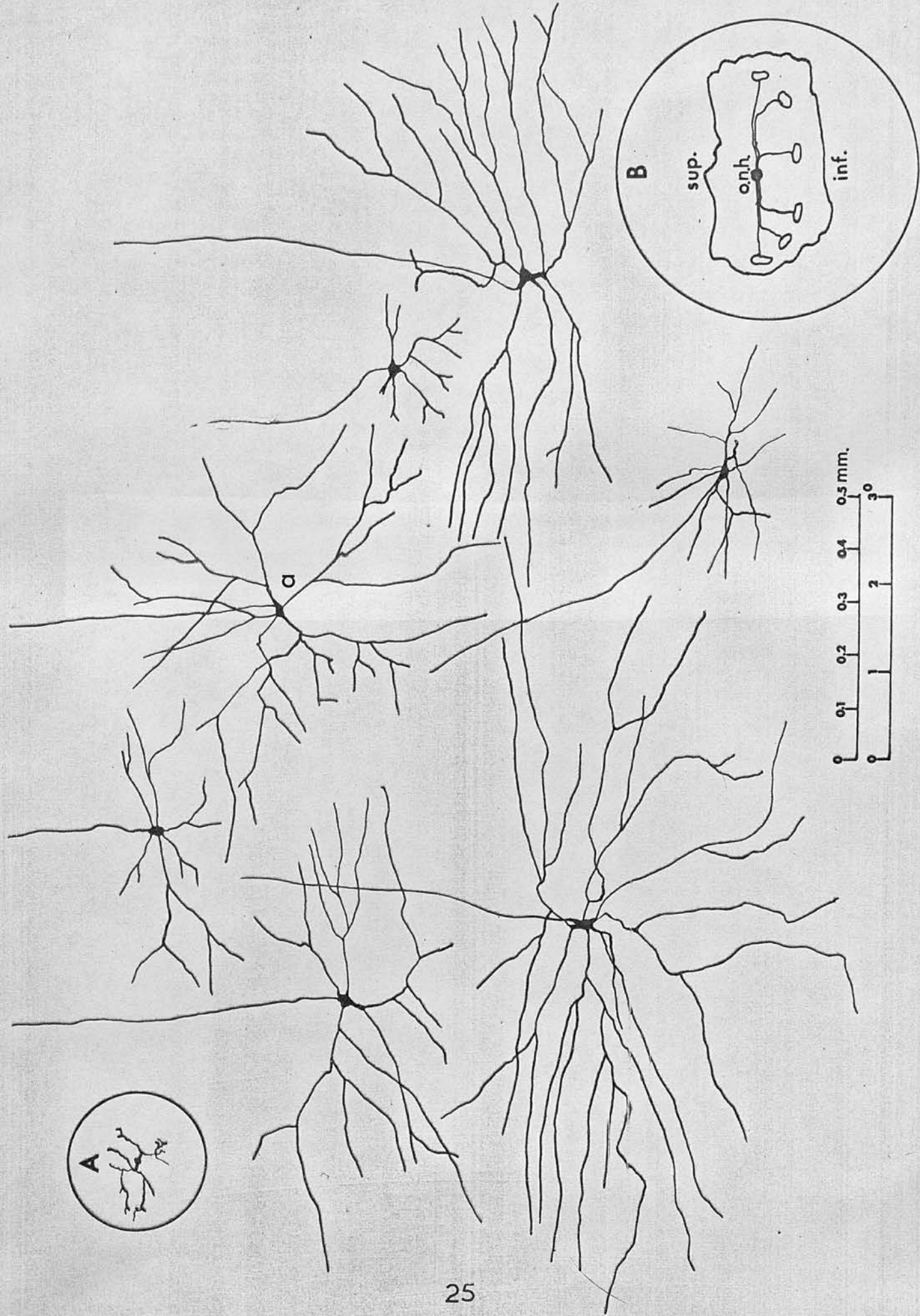
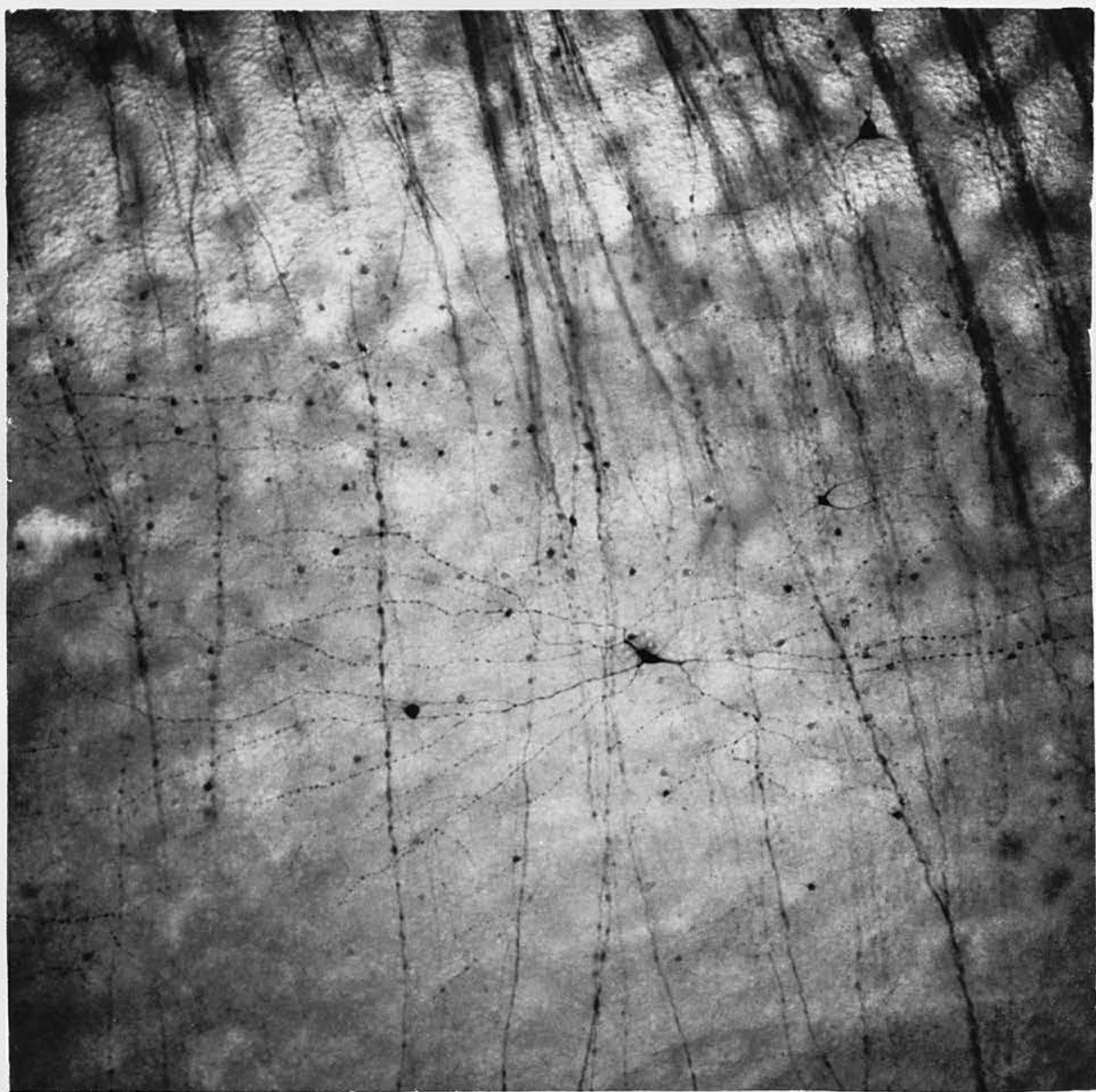


Fig. 26 Is a photograph of an 'in vivo' stained ganglion cell (methylene blue). The major axis is parallel to the projection of the horizon on the retina and at right angles to the bundles of axons seen passing down the retina from the myelinated band. Magnification x 100.



TOPOGRAPHIC DISTRIBUTION OF RETINAL CELLS

GANGLION CELL DISTRIBUTION

Introduction. The retinal image of the visual field is of fairly uniform magnification in the rabbit. It was shown earlier that the image of regions 60° nasal and temporal of the optic axis is compressed about 20% more than the image of a region on the optic axis. All parts of the rabbit visual system are in strict topographic relationship to the retinal receptor mosaic. The neural activity generated by the image of the visual field is thus organised in such a fashion that the visual field may be said to have a projection within the CNS. The differential transformation of the central visual field projection at various levels of the visual pathway can give clues as to the fashion in which an animal handles its visual input. In this section the ganglion cell layer will be described; the ganglion cell density gives the output per unit area of the retina. The operations carried out in the receptor and bipolar layers of the retina will be dealt with later.

The retina of the rabbit is very characteristically organised. The optic nerve fibres do not spread evenly over the retina but, after leaving the optic nerve head, run nasally and temporally in a band, about 8° wide, which disappears peripherally at points projecting into the visual field on the nasal and temporal 60° vertical meridia. The band lies with its centre some 20° above the horizontal. At the projection of the horizontal on to the retinal surface is found the 'visual streak' which was described by Chievitz (1891). All the retinal layers are thickened in this region and for a detailed description the reader is referred to Prince (1964). The visual streak, which is the area centralis of the rabbit, cannot be easily observed by the use of an ophthalmoscope and is best defined by a count of the ganglion cell density throughout the retina. The count may be carried out on either a serial sectioned retina or on a squash mount. The former technique is tedious and requires considerable care in sampling (Abercrombie, 1946; Marrable, 1962). The method was used by Seneviratne (1963) to reconstruct part of the streak region from serial sections but no corrections were made and only relative counts are quoted. It was thus determined that

a /

a retinal ganglion cell density map should be made from a squash mount preparation.

Methods.

Shrinkage.

Details of the preparation of whole mounts are given in the methods section. The dissected retina was fixed on a gelatinized slide in formalin vapour. Such fixation causes little shrinkage (Østerberg, 1935). Van Buren (1963) estimates a 6% change in linear dimensions of the retina. Dehydration before balsam mounting may introduce up to 25% decrease in linear dimensions but this change may be avoided if the retina is firmly adherent to the slide after fixation. Slides showing tearing or rumpling during dehydration were disposed of. The slide numbered RR7 was the most successful and the following description is based upon its appearance. A few retinas were mounted in gelatine for other purposes but their peak counts on the streak region differed little from those of the balsam series so that shrinkage cannot have been very great in the latter group. No attempt has been made to correct counts for shrinkage so that this must be borne in mind during their examination. A photograph of preparation RR7 was cut out and reassembled, with great ease, to form a hemisphere which suggests that any shrinkage that occurred was similar along horizontal and vertical axes.

Counting.

The number of cells within the whole field of the microscope was counted at a total magnification of 1,570. The count at several adjacent points was averaged and converted to a value representing the count within one square millimeter. The position of the counts was read off from the stage micrometer and the value was inserted on an enlarged photograph of the preparation. Isocount lines were drawn in surrounding all regions with a count above some value and excluding those below. There was little difficulty in the identification of the ganglion cells during counting. Nearly all possessed a clearly visible nucleolus and deeply stained Nissl substance.

Results.

Ganglion /

Ganglion cell density map.

Figures 27 and 29 show the appearance of the complete ganglion cell density map. The principal feature of the map is the uniformity of the count along the horizontal. In the preparation RR7, the retina shown in the diagram corresponds to about 190° of visual field and yet, for its whole length, the distribution of the isocount lines remains almost unaltered. The expansion of the 1,000 count line in the temporal retina corresponds to the region of the binocular field but comes about as the result of the disappearance of the myelinated fibre band. The count falls off rapidly in the vertical plane as the optic nerve head is approached from the region of highest count and the upper retina, which deals with the ground, has a very low count of 300 g.cell/mm². In passing down the retina from the streak the count decreases much less rapidly and remains at 500 g.cell/mm² at a distance of 7 mm below the streak. This region deals with the upper field and with the overhead binocular area.

The peak count within the area centralis falls along the middle of the strip and is uniform at about 5,000 cells/mm² for almost the entire length. Figure 30 shows the distribution of the ganglion cells along the vertical axis of the retina for various regions along the horizontal axis both nasal and temporal of the optic axis. The peak count along the vertical at the optic axis is used as a reference point. It is clear that the peaks lie in a straight line except at the limits of the retina where distortions introduced by flattening the retina will be most noticeable.

Table II indicates the percentage of the total ganglion cell count found within each isocount line for three preparations. The uniformity is marked. Data for the cat is included and was taken from Stone's paper (1965). The average of the total ganglion cell count for the three animals is 242,000 but the sample of cells counted was rather too small for this to be very reliable.

Discussion. Stone finds the area centralis of the cat to be most consistent from animal to animal if defined as the region encircled by the 3,000 g.cell/mm² isocount line (1965). The relatively enormous size of the rabbit /

TABLE II

Distribution of retinal ganglion cells within isocount lines

Region	Rabbit RR7 No. G cell $\times 10^3$	% of Total	Rabbit RR9 No. G cell $\times 10^3$	% of Total	Rabbit RR10 No. G cell $\times 10^3$	% of Total	Cat No. G cell $\times 10^3$	% of Total
Without 1,000 g. cell/mm ²	60	21	48	20	50	21	53.4	74
Within 1,000 g. cell/mm ²	224	79	180	80	185	79	18.6	26
Within 2,000 g. cell/mm ²	156	55	136	60	119	51	10.4	14
Within 3,000 g. cell/mm ²	81	29	86	38	61	26	3.7	5
Total Count (No. g. cell in retina)	284,000		228,000		235,000		90,000	[#]

N.B. [#] Total here is that quoted by Stone (1965). Breakdown of count for cat was estimated crudely from isocount areas in one of Stone's diagrams (Total in this case was 72,000).

rabbit area centralis is obvious upon comparison with Stone's figures for the cat. The area centralis of the cat is 0.91 mm^2 in area and contains about 5.5% of the retinal ganglion cells. The total count for the region within the 3,000 isocount line has not been made in the rabbit but we may assume a uniform distribution of 3,000 g.cell/ mm^2 . The area centralis of the rabbit is thus found to contain at least 29% of the retinal ganglion cells and to have an area of 23.3 mm^2 . The rabbit area centralis is consequently 26 times greater in area than the equivalent region of the cat and contains nearly as many cells as the whole cat retina. The cat area centralis is shown in fig. 27a as an insert on the same scale as the rabbit retina.

GANGLION CELL SIZE DISTRIBUTION

Introduction. The ganglion cell density map reveals the presence of a specialised area centralis in the rabbit retina. Levick (1967) has reported that the cells of this region possess rather specialised properties when compared with those of more peripheral areas. It appeared likely that this specialisation might be reflected in the nature of the ganglion cell population of the region. A detailed study of the three dimensional organisation of the ganglion cell dendritic trees was rejected in favour of a simply carried out survey of ganglion cell diameter in various regions of the retina.

Method. The diameter of ganglion cells was measured at a magnification of x 500 on microphotographs of 8 regions of area 0.3 mm^2 and spaced at intervals of 1 mm along a vertical line passing through the optic nerve head at right angles to the visual streak. The retina used for the measurements was fixed, but not dehydrated, and mounted in gelatine. 4,500 cells were classed into 6 groups of diameters ($0-5\mu$, $6-10\mu$, $11-15\mu$, $16-20\mu$, $21-25\mu$ and 25μ), which are similar to those used by Stone (1965), so that the results obtained are comparable with those obtained from the cat.

The cell diameter distribution of two regions was redetermined at greater resolution in order to test for uniformity of the distribution. 827 cells were /

were measured at the region of density $2,700 \text{ cell/mm}^2$ while measurements of 237 cells in the 760 cells/mm^2 area and 219 cells in the 660 cell/mm^2 area were averaged to give a more representative population. The major axis of the cell and that of one at right angles to it were measured and averaged as an indicator of diameter distribution within the population. The counts are displayed as the percentage of the total contributed by groups of cells at 2μ diameter intervals. The cells from the region near the streak show a unimodal distribution of diameter (fig 31a). The peripheral cells show a much broader distribution in which three components, at least, are suggested (fig 31b). The distribution will be referred to in the section on the optic nerve count.

Results. The density of the different ganglion cell size groups at various points along the vertical axis is shown in fig. 32. Figure 33 portrays the same results expressed more conveniently as the percentage frequency of the various cell diameter groups at regions of different ganglion cell density. The appearance of a region near the streak and one 8 mm away is shown in photographs 34 and 35 respectively.

Discussion. The results from the rabbit are quite different from those of the cat. The two classes 5-10 μ and 11-15 μ form an almost constant 50% and 30% respectively of the total count at almost all cell densities. The 16-20 μ group is poorly represented at the streak but rapidly increases its contribution towards the inferior retina and remains almost constant until the periphery is reached. The large cells of group 21-25 μ and >25 μ show a marked increase as the periphery is approached but the contribution does not reach 10% in the most peripheral sample. In the cat the 6-15 μ group is not uniformly represented but is reduced to 15% of the total by the $1,000 \text{ cell/mm}^2$ isocount line. The decline in small cell count towards the periphery is accompanied by an increase in that of the large cells; the 16-20 μ class forms 50% of the total at the $1,000 \text{ cell/mm}^2$ margin. The rabbit retina thus demonstrates a much more constant distribution of ganglion cell size than is found in the cat when passing from the area centralis to the periphery.

Similar counts have not been carried out along other lines passing perpendicular /

perpendicular to the streak at points nasal and temporal to the region examined above. The similarity of the total count distributions (fig. 29) for these regions suggests, however, that their cell diameter distribution will be similar to that described above. Examination of the retina certainly does not reveal any differences in the cell distributions to the casual observer.

RECEPTOR, BIPOLAR AND GANGLION CELL RATIO COUNTS

Introduction. The investigation of the distribution of ganglion cell diameters in the rabbit area centralis revealed, unlike the case of the cat, no marked characteristic difference, other than a somewhat greater homogeneity, from that of the peripheral retina. In fact, if homogeneity of ganglion cell size, and thus presumably of dendritic tree size, were assumed indicative of homogeneity of function then the results described in the previous section would suggest that a greater variety of unit types would be found in the periphery than at the area centralis. In the search for clues about the organisation of the streak region it was decided that counts of receptors, inner nuclear layer cells and ganglion cells should be carried out at various points below the optic nerve head and that the ratio of the various cell types should be determined for each region. No attempt was made to distinguish horizontal, amacrine and bipolar cells in the inner nuclear layer, so that the phrase "bipolar count" should be understood to include horizontal and amacrine cell nuclei as well as bipolar nuclei. Two sections were analysed in this fashion. The results were in agreement and those from one section are presented below.

Method. Microphotographs were taken of 14 regions of the retina situated at various distances below the optic nerve head. Each photograph depicted 0.35 mm of retina at a magnification of x 80. The sections were 10 μ thick. A count of receptors was made to check against the receptor nuclear count which was difficult to carry out on photographs because of the limited depth of focus at the required magnification. The results were in agreement. The /

The counts were subjected to an Abercrombie correction (Abercrombie, 1946) on the assumption that rod nuclei are 2.5μ , bipolar nuclei 6.6μ and ganglion cell nuclei 9.5μ in diameter. The latter diameter is not in accord with the findings of the distribution in the non-dehydrated preparation but the counts were carried out on paraffin embedded material so nuclear diameter was estimated from the photographs. Figure 36 shows photographs of various regions of the section examined.

The receptor, bipolar and ganglion cell counts after the Abercrombie correction are shown in figures 34, b and c. Note the coincidence of the peaks in the receptor and bipolar counts with the region of the streak indicated in the ganglion cell count. There is a marked parallelism of the receptor and bipolar curves which both show a peak followed by a maintained plateau in contrast to the ganglion cell count which drops away rapidly.

The ratios of the counts are shown in fig. 38. The receptor count to bipolar ratio is constant at a value of about 11 through most of the retina. The ratio increases to a value of 16 at the region under the margins of the myelinated band. This perhaps increases sensitivity in the area. The ratio decreases to a value of about 9 in the region of the streak.

In contrast, the bipolar to ganglion cell ratio shows a much more marked decrease at the streak which results from the disproportionate increase in the ganglion cell count relative to that of the bipolar increment. Note the plateau in the bipolar / ganglion cell curve which extends for about 5 mm along the retina to end at the $1,000$ ganglion cells/mm² region. The constancy of the receptor / bipolar ratio results in the overall receptor / ganglion cell ratio curve possessing a form similar to that of the bipolar / ganglion cell ratio. The enormous change in the receptor / ganglion cell ratio in passing from the streak (35:1) to the periphery (600:1) should be noted.

Discussion. The peaks in the plots of the receptor and bipolar counts reveal that the streak is represented, albeit not so markedly, in these layers as well as in the ganglion cell lamina. The potential increment in resolution offered by the increased receptor density on the streak may not be lost at the bipolar /

bipolar level because the bipolar count shows a parallel increase. The constancy of the receptor to bipolar ratio throughout the retina may indicate that the outer plexiform layer performs a uniform function in all areas. It appears likely that the cells of the outer and inner nuclear layers are organised into subunits of uniform composition, or at least into subunits of different composition but uniform distribution, throughout the retina. The slight excess of inner nuclear layer cells over receptors at the streak may indicate a lesser degree of convergent connections from the receptors to the bipolars. Such an arrangement might be expected if the cone population of the streak is significant as is suggested below. It may be, however, that the amacrine and horizontal cell population become greater in these regions for those cells were lumped together with the bipolars in counting.

The uniformity of the receptor to bipolar ratio suggests that the specialisation of the streak region in these two layers is possibly only reflected in the higher densities of cells and not in their more complex interconnection. The increment bipolar count at the streak is little more than that necessary to maintain the constant ratio with the receptors and is thus probably subsequent upon the increased receptor density which brings about the higher acuity, or increased sensitivity, of the area centralis. It appears that we must look to the organisation of the inner plexiform layer for the anatomical substrate of the more sophisticated single units recorded from the visual streak.

It is not possible to say more about the specialisation of the streak region without extensive, less gross, quantitative data. Detailed investigation of EM serial sections offers the most satisfactory approach even if it is the most time consuming.

Chievitz (1897) carried out a similar count to the above on the cat. His results have been plotted [REDACTED] along the equator of the cat retina. The same tendency for a uniform receptor / bipolar ratio as is found in the rabbit appears in the plot. The plateau in the bipolar / ganglion cell ratio is also apparent.

Cone /

Cone distribution.

Prince (1964) refers to cones as being present in high concentration along the rabbit visual streak. Some observations made on the photographs used for the above count offer possible evidence in support of his view. It was noticed that photographs of the streak bore patches of receptor outer segments which were less well stained than their neighbours. Such patches were not observed in more distant regions (compare figs. 36a & b). The receptors in the patches were apparently thicker than the neighbouring rods. The clumps were especially noticeable because they occurred in association with expansions of the pigment cells. The receptor expansion was visible only at the outer $\frac{1}{3}$ to $\frac{1}{4}$ of the layer of outer segments. It is appreciated that these elements may be angled sections through rods or distortions produced during cutting because of different mechanical properties of the regions. The appearance of the expansions brings to mind, however, that of the type II receptor found in sections examined under the electron microscope (fig. 10). This resemblance is enhanced by the obvious association of the receptor expansions with pigment cells (fig. 36a). A count of the clearly defined clumps of receptor expansions was made in various regions of the retina. The distribution is shown in fig. 37d. The presumed cones are concentrated on the streak region. It is likely that these cells are the atypical cones described earlier which contribute the photopic phase of the ERG. An EM examination of the area is intended.

Fig. 27 Diagram of an 'in vivo' methylene blue stained squash mount of a rabbit retina superimposed with the isocount lines of a ganglion cell density map. The hatched area indicates the myelinated band of fibres which pass to the optic nerve head. The vertical dotted line indicates the vertical meridian which passes through the optic nerve head. Figures on the left indicate the isocount line values in number of ganglion cells per square mm. Left eye.

The inset shows, to the same scale, the ganglion cell distribution within the 3,000 g.cell/mm² line of the cat retina.

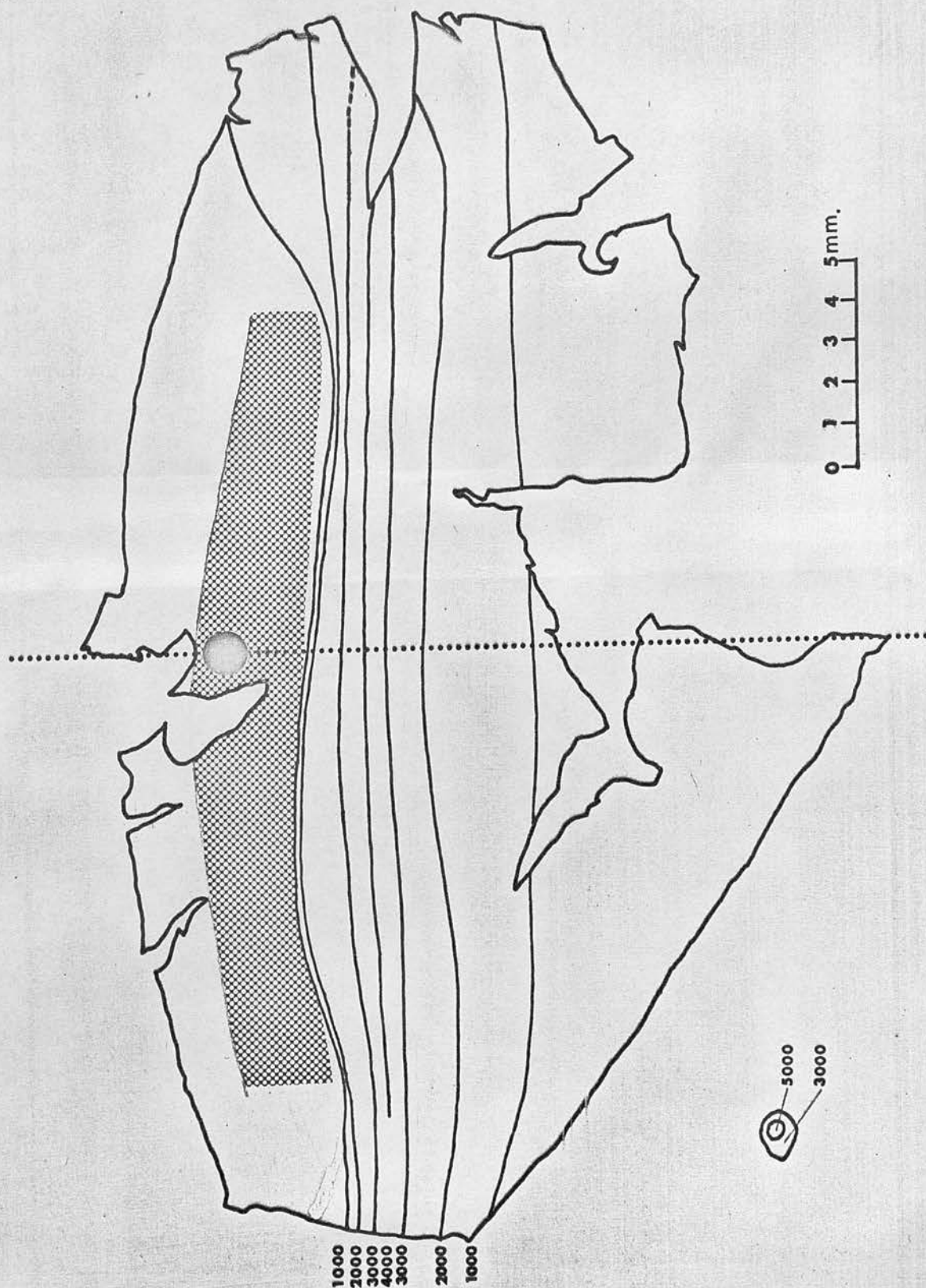


Fig. 28 A photograph of the retina shown in the previous diagram. The region of high ganglion cell density has, for an unknown reason, come out white in the photograph. Note the expansion at the temporal end of the retina.



Fig. 29 Another squash mount isocount diagram. Legend as for fig. 27.

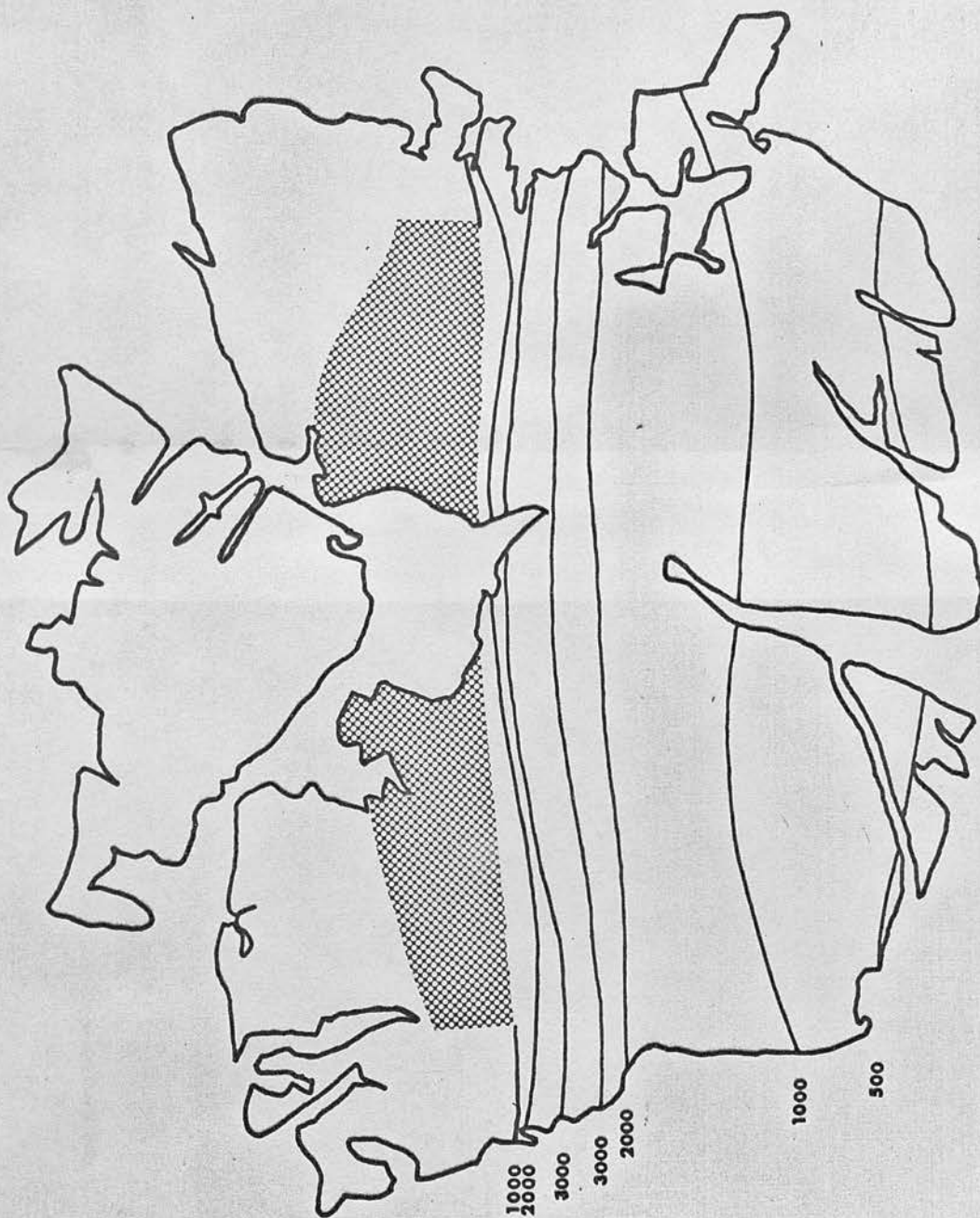


Fig. 30 The ganglion cell concentration is shown from top to bottom of the retina for vertical sections at various distances from the optic nerve head. The arrow and dotted line indicate the level of the peak count in the section passing nearest to the vertical meridian passing through the optic nerve head.

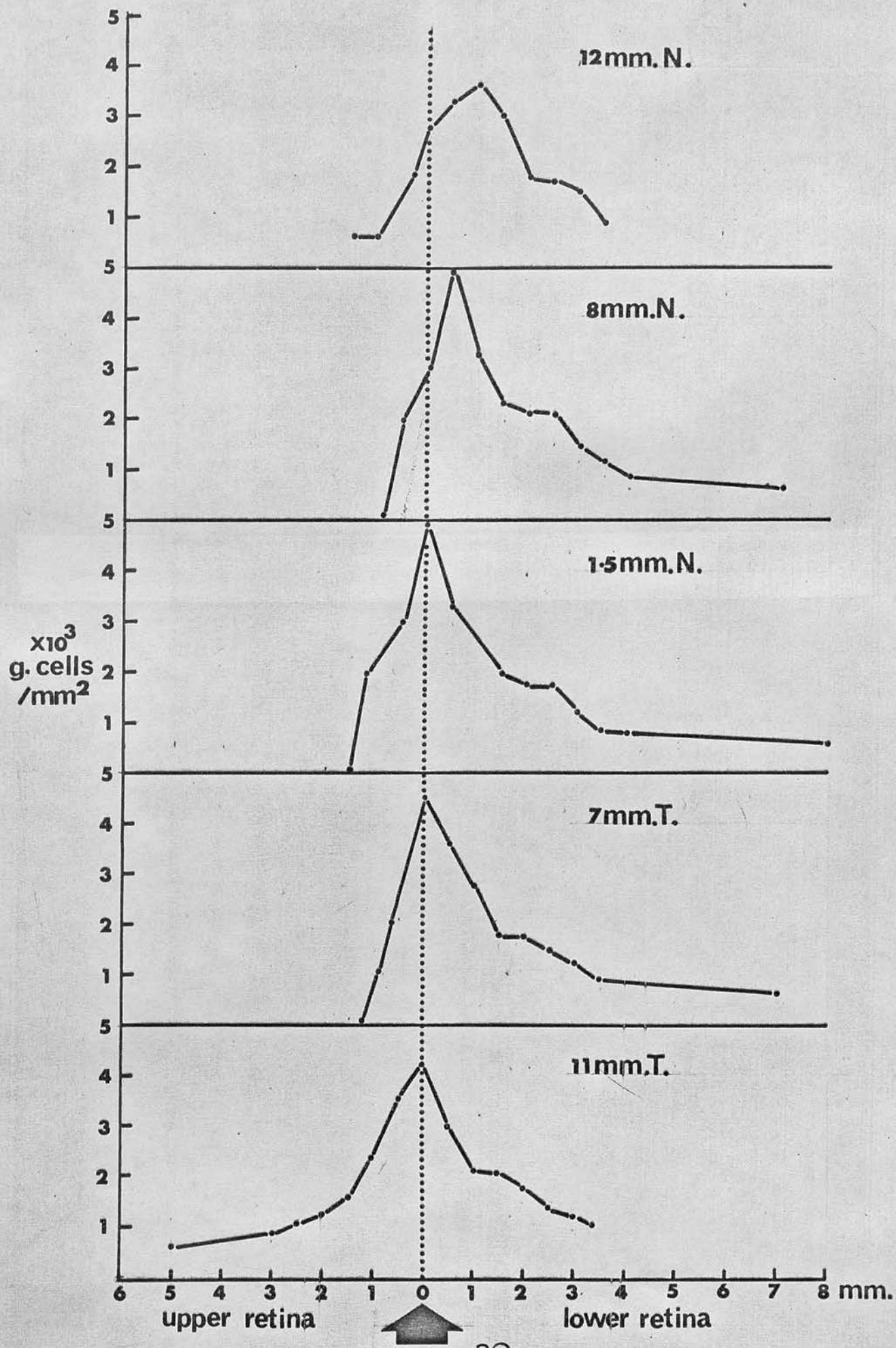


Fig. 31 High resolution histogram of the distribution of ganglion cell diameters at the streak and in the periphery 9-8 mm. below the streak.

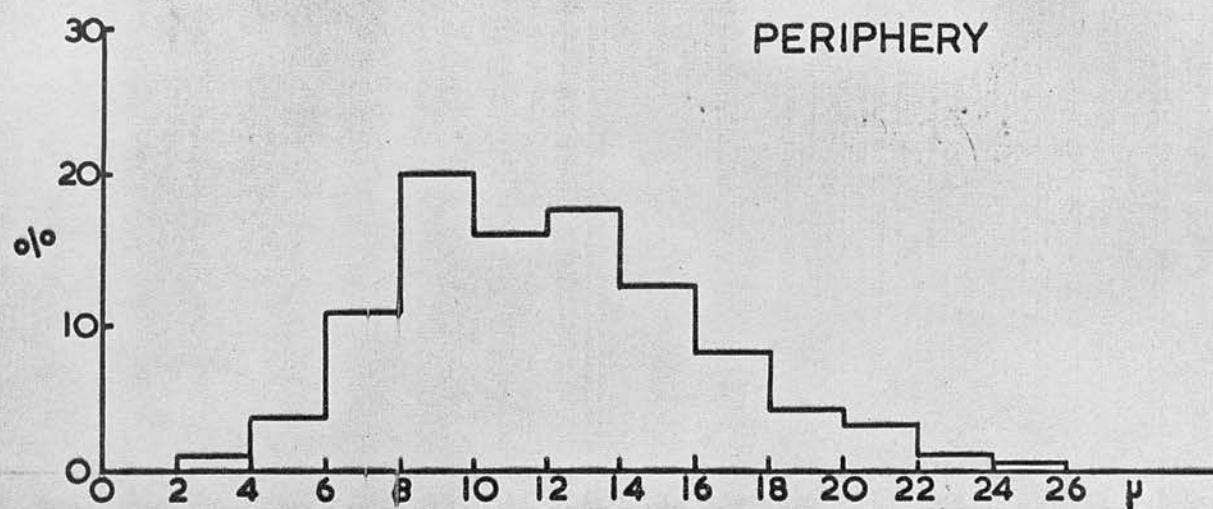
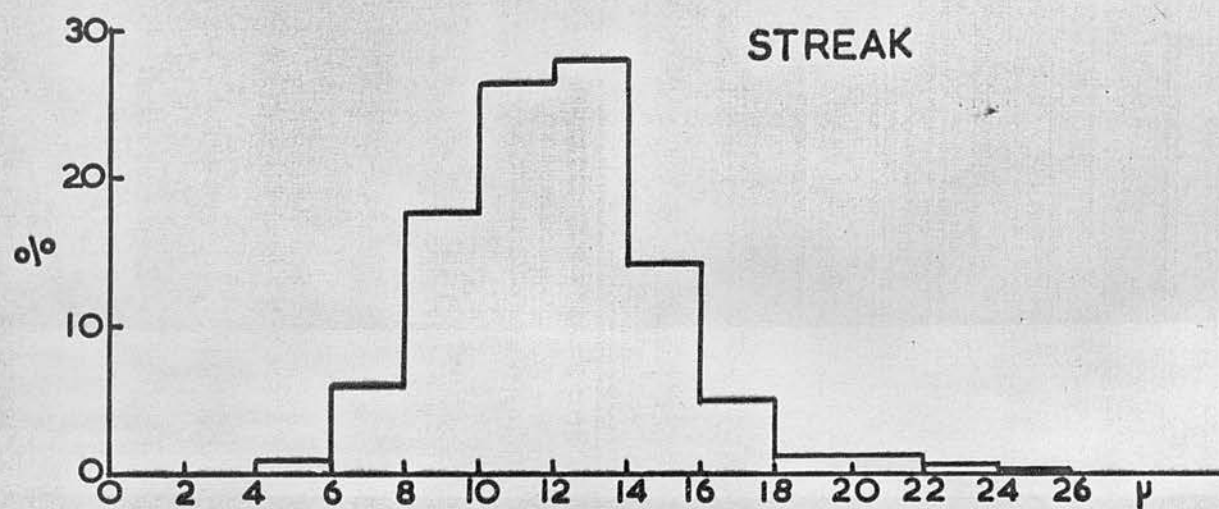


Fig. 32 Number of ganglion cells in each of the five classes of diameter selected by Stone (1965), in the case of the cat, at various regions of the vertical meridian which passes through the optic nerve head. Note that the distribution in the upper retina is similar to that in the peripheral lower retina.

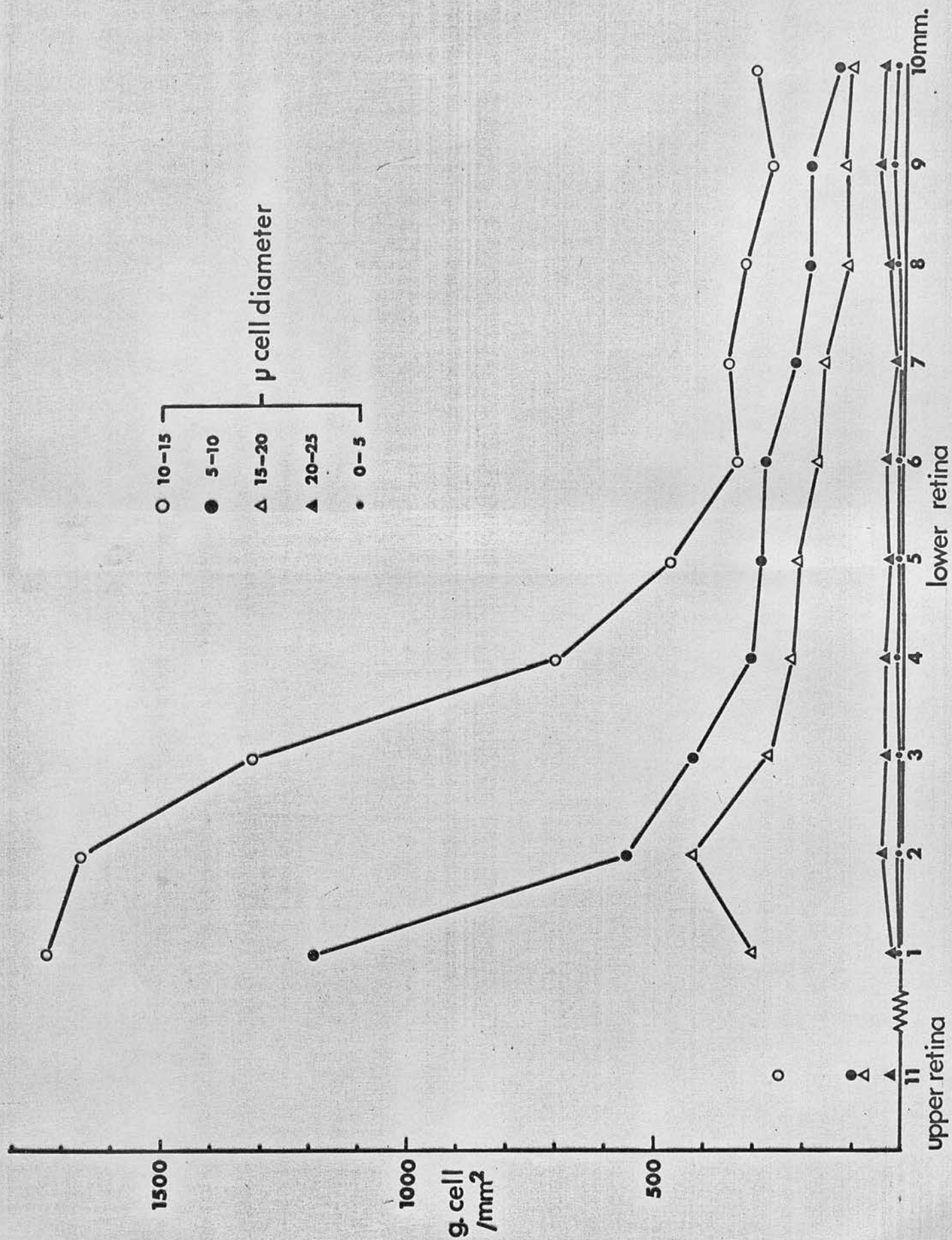


Fig. 33 The data of fig. 32 shown in terms of the percentage of all the cells at a given counting region in each of the five diameter classes.

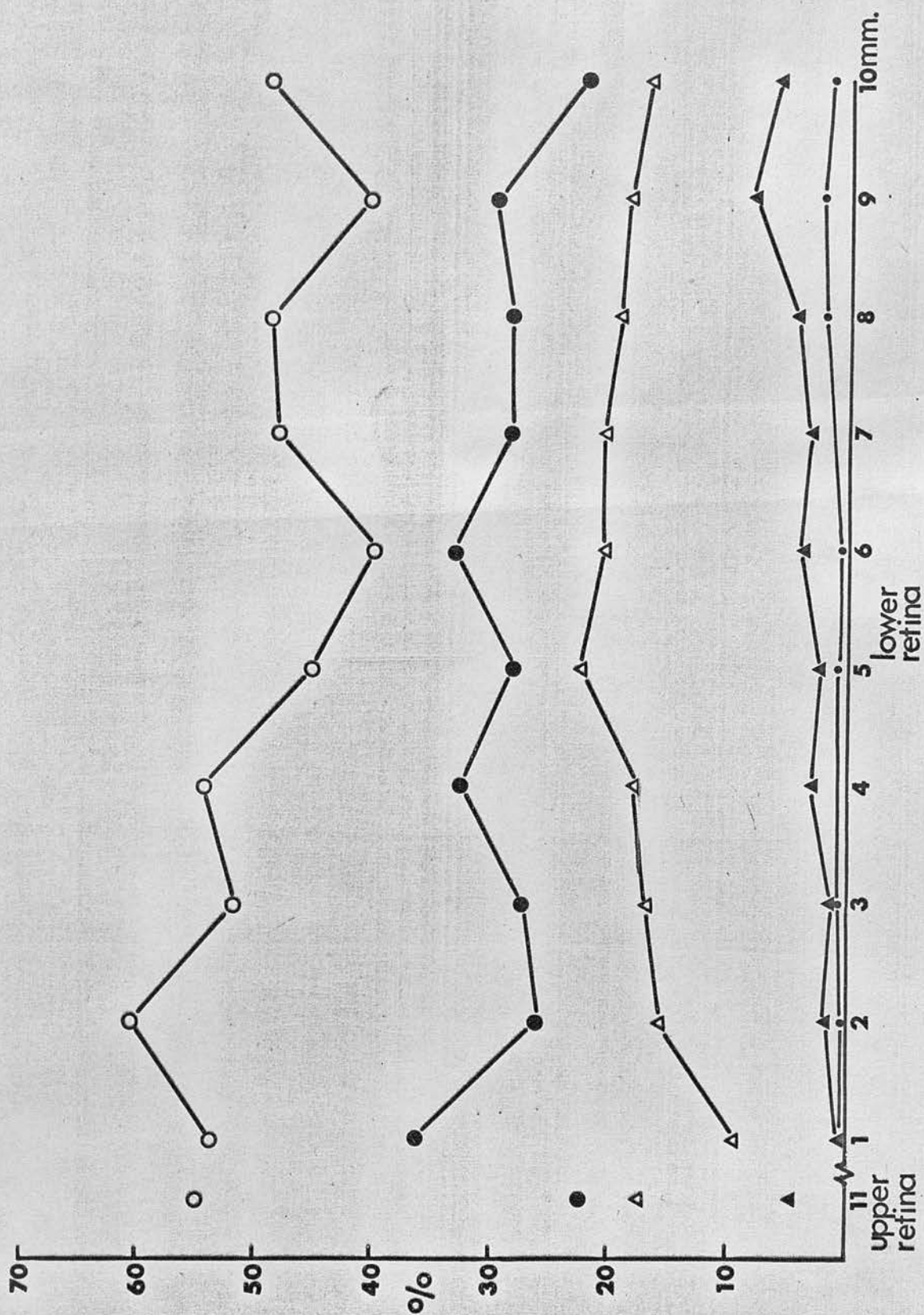


Fig. 34 The appearance of a region of retina close to the visual streak. The streak is towards the bottom of the page. The retina was stained in vitro with methylene blue and squash mounted.

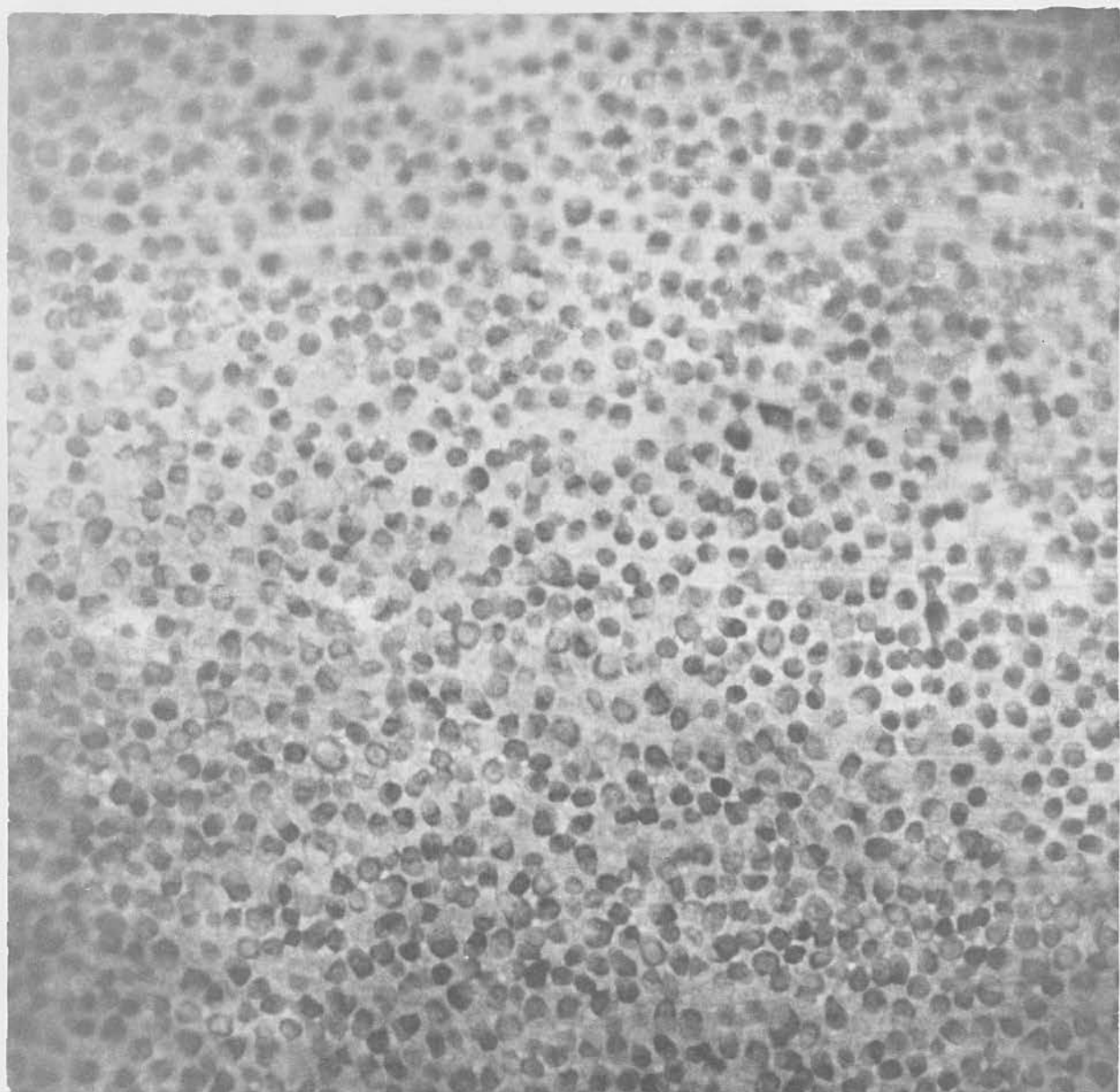


Fig. 35 A similar photograph to the above but of a region 8 mm. below on the retina. Magnification is approximately 300.

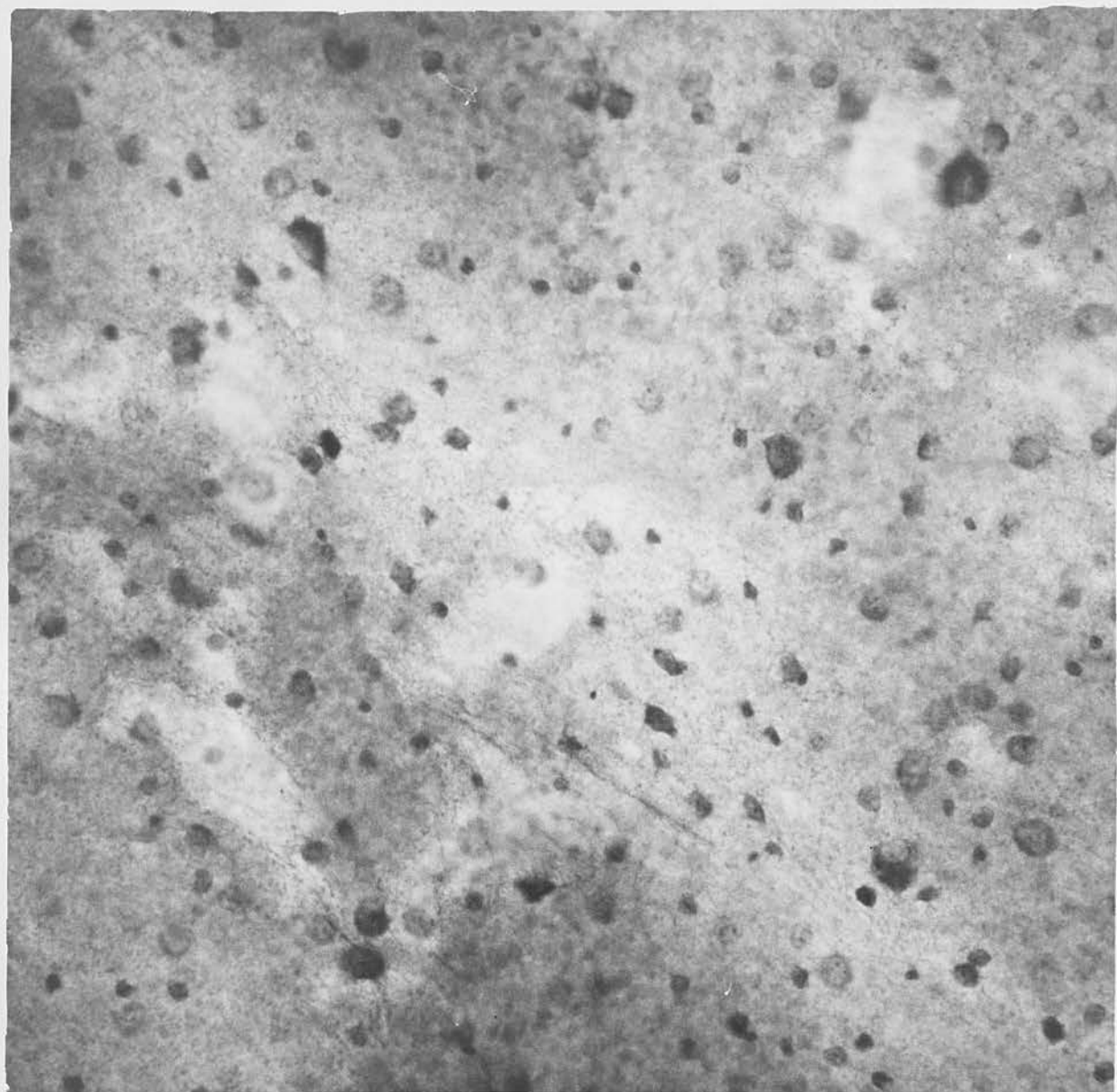
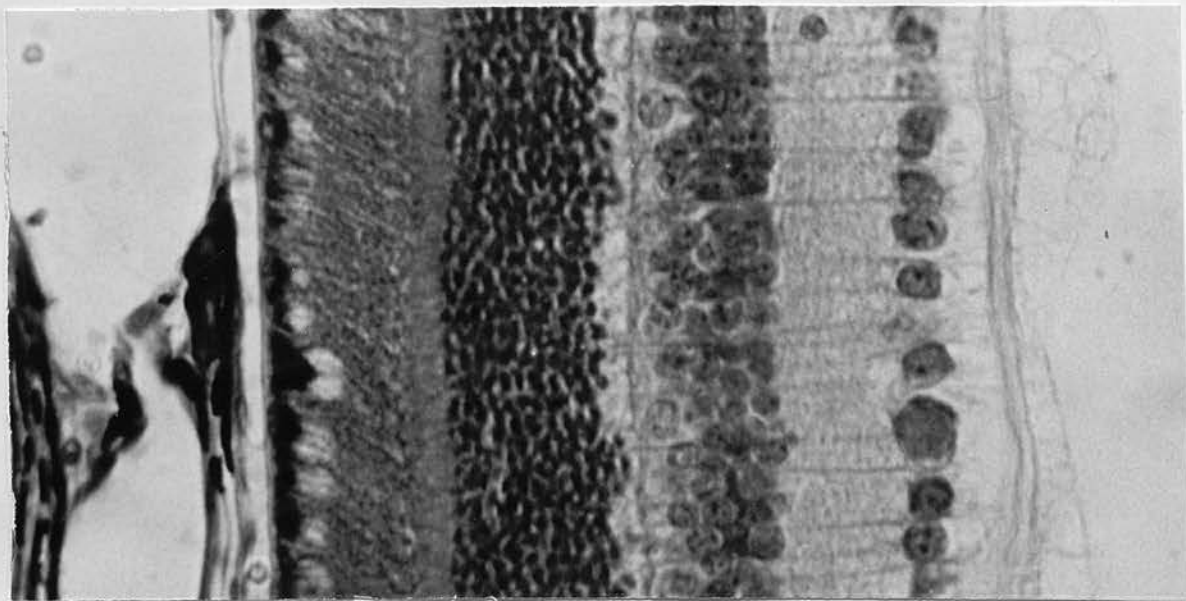
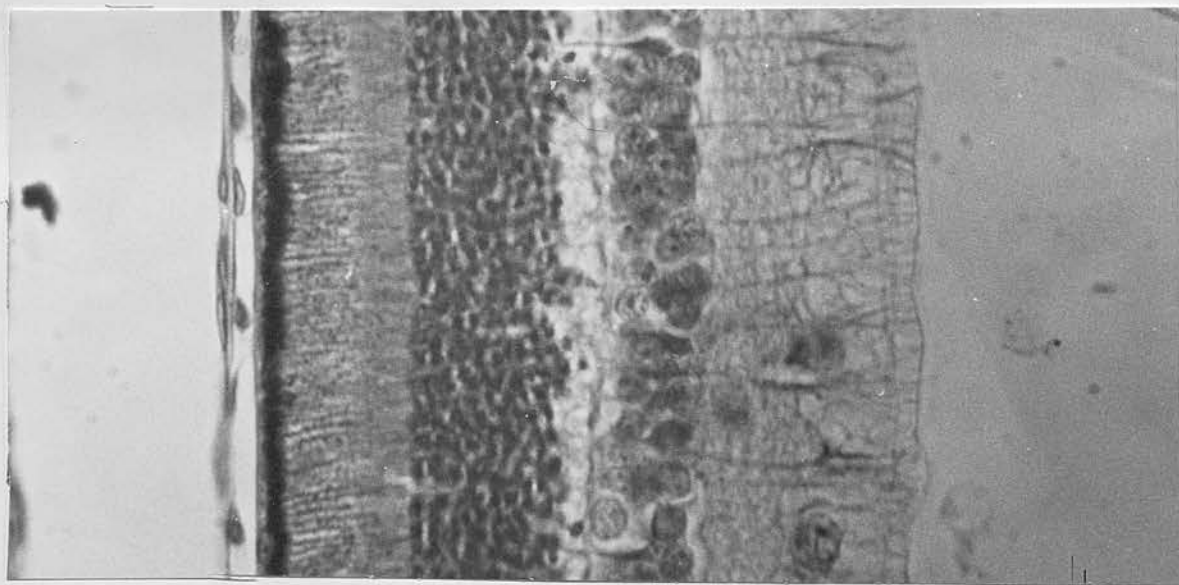


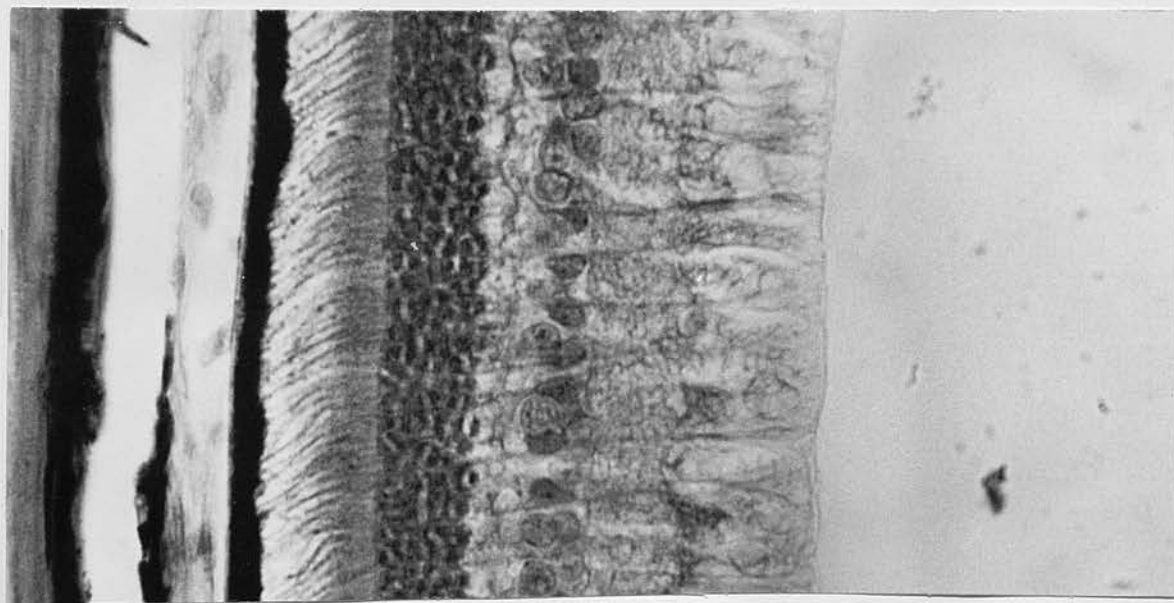
Fig. 36 Radial sections of retina taken parallel to the vertical meridian at various levels. Note the thinning of the inner and outer nuclear layers as the periphery is approached. Magnification 600.



Streak



2.5mm below streak



11.5mm below streak

Fig. 37 Distribution of the absolute counts of receptors, bipolars, and ganglion cells from immediately below the myelinated band to the periphery 17 mm. below on the vertical meridian passing through the optic nerve head. Note the representation of the streak in the peak count at the receptor and bipolar levels.

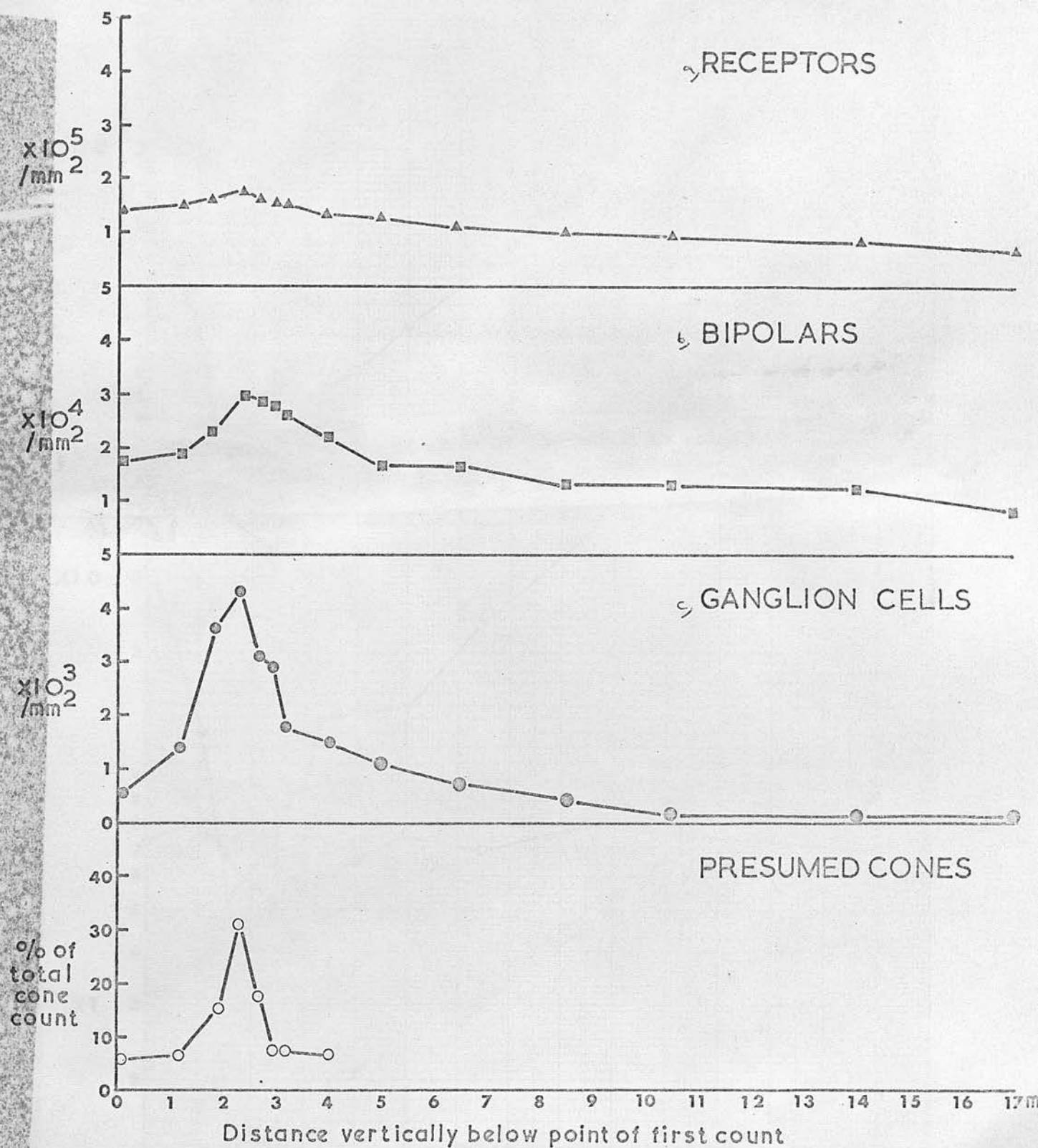


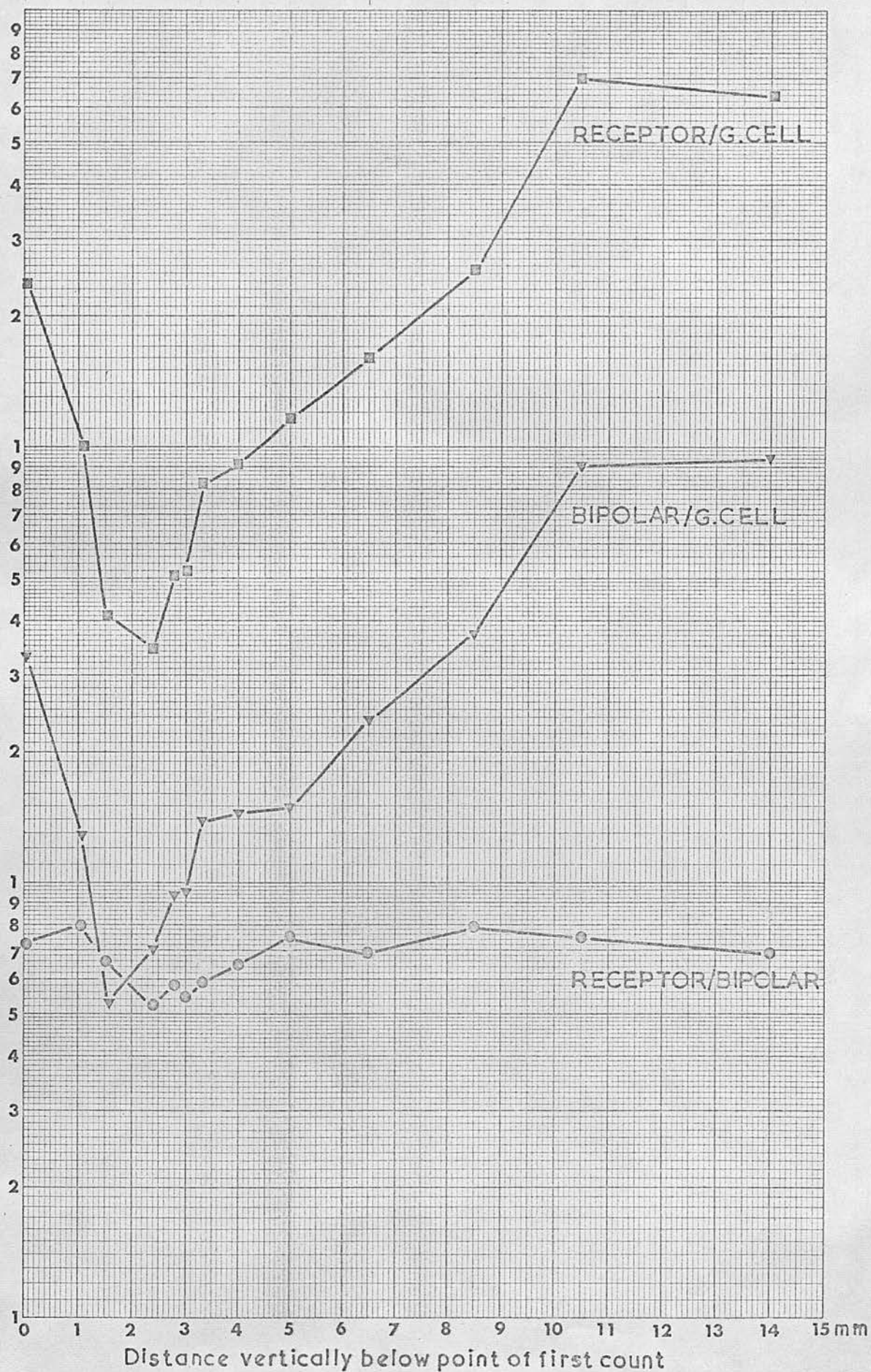
Fig. 38 The ratio of the number of cells in outer nuclear, inner nuclear and ganglion cell layers.

CINTEC L. GRAPH SHEET No. 5531
LOG 3 CYCLES X MM. 1/4" & 1 CM.

X100

X10

X1



OPTIC NERVE FIBRE COUNT

The literature contains no description of an axon count which has been carried out on the rabbit optic nerve with an electron microscope. In view of Maturana's recent unexpected discovery of the presence of a large number of unmyelinated fibres, which had not been observed by light microscopy, in the frog optic nerve, it was decided that a total count and diameter distribution would be determined by means of the electron microscope for the axons of the rabbit optic nerve.

METHODS

The following counts were carried out on one optic nerve taken from an adult rabbit. The nerve was fixed in vivo by perfusion with gluteraldehyde. It was removed from the animal, soaked in a buffered osmium tetroxide solution (see methods appendix) and mounted in Araldite. Other methods of fixation were tried but in all cases the nerve core was poorly preserved. The fibres at the core of the nerve used for this count showed sheath breakdown (fig. 39) but the axon outline and parts of the sheath remained so that the outline could be reconstituted. The region treated in this fashion showed a similar fibre diameter distribution to well preserved areas adjacent to it and was consequently included in the count.

0.5-1.0 μ thick sections were cut across the whole nerve after it had been mounted on the ultra-microtome. The whole section was photographed at known magnification (fig. 41) and printed on a sheet of measured area. The photograph was weighed before and after the image of the nerve had been cut out. The area of the nerve cross section was then calculated to be 1.49 mm².

The face of the ultra-microtome block was then trimmed down in order to cut thin sections for EM use. The orientation of the nerve had been noted and it was arranged that a strip running from top to bottom of the nerve remained intact. After counterstaining, the sections were placed in the EM and a series of photographs was taken of a strip, 25 μ wide, running from top to bottom of the nerve. Each photograph overlapped the next slightly and 60 were required; alternate pictures were used for the present count. A calibration /

calibration grid ($2,160 \text{ lines/mm}^2$) was photographed at the same magnification. Enlargements for counting the fibres were made at a total magnification of 10,000.

The cross section of the optic nerve fibres is not circular. Forrester and Peters (1967) used the mean of the major and minor axes as an index of diameter. That method is tedious to carry out. It was found, however, that accurate estimates of cross sectional area could be made by an observer matching axonal area to holes cut in a cord which were of such dimensions that they represented the cross section of circular fibres from 0.5μ to 7.0μ in diameter at 0.5μ steps. Extra holes were added for 1.25μ and 1.75μ in order to define the peak of the distribution more accurately. In this fashion 1,612 fibres were classed according to diameter. A further 4,398 fibres were counted without classification according to size. The sum of the areas represented on the photographs was divided into the optic nerve cross sectional area and the product with the nerve fibre count was formed.

RESULTS

The total count for the nerve was found to be 276,000 fibres which is in good agreement with Bruesch and Arey's estimate of 261,000 and 265,000 fibres (1942) in spite of the fact that their count was carried out with the light microscope. Considering the fact that the previously obtained ganglion cell count was achieved in a crude fashion then the agreement (average of three 250,000) with the optic nerve count is quite fair. No deductions about the presence or absence of centrifugal fibres could, however, be based upon the results.

Fibre diameter distribution. The distribution of the diameters of the circles of equivalent cross sectional area to the axons is given in figure 42a. The measurements include the thickness of the myelin sheath. The modal diameter is 1.5μ and no significant secondary peaks appear. The range is from 0.5μ to 6.5μ and about 85% of the fibres are less than 3.0μ in equivalent diameter. More than 90% are greater than 1.0μ .

In /

In order to determine whether the fibre diameter spectrum was different for the streak, upper and lower retina, the strip of optic nerve was divided into 3 equal parts and about 350 fibres sampled from each. The distributions are shown in fig. 42. The modal diameter in all cases is 1.5μ and little difference is apparent between the regions or between any region and the overall spectrum. A slight secondary hump appears in the curve for the lower nerve at about 3.3μ . This may correlate with the changed composition of the ganglion cell diameter distribution for the region of the lower retina to which, as is shown in the inserts (fig. 42), this portion of the nerve corresponds (Brouwer, 1923). The results show the uniformity which would be predicted from the distribution of cell diameters within the retina.

Unmyelinated fibres. Arey and Schaible (1934) counted 261,000 fibres of which 18% were described as unmyelinated. Bruesch and Arey (1942) found 265,000 fibres with silver stain and 261,000 with an osmic stain. They attribute the early results to poor preservation by the osmic acid and deny the existence of unmyelinated fibres. Knoche (1960) assessed about 2.5% unmyelinated fibres concentrated around the periphery and apparently passing to the hypothalamus. A small number of such fibres were found at the very periphery of the nerve in the present study but no attempt was made to count them as a significant sample was not available.

DISCUSSION

Conduction velocity. Bishop (1933) describes two, rather variable, peaks in the response of the rabbit optic nerve to electrical stimulation. The fastest fibres possessed a conduction velocity of from 50-20 m/sec. The second peak contained fibres in the 14-7 m/sec. group. A low, diffuse, hump was mentioned as having a conduction velocity of about 4 m/sec.

Granit and Marg (1958) describe peaks in the compound action potential of the rabbit optic nerve at 56, 36, 23, 16 and 10-5 m/sec. The maximum recorded conduction velocity for the leading edge of the wave was 65 m/sec. Studies were made on the latency of groups of retinal spikes responding to optic /

optic nerve stimulation but no attempt was made to identify the conduction velocities. A broad spectrum of latencies was observed with a few peaks in the distribution.

Synthesis of observations. The optic nerve axon diameter distribution described above is not in agreement with that of Yuri(1960). He describes the rabbit distribution as being the same as that of mice and as having a range of 0.1 to 3.0 μ in diameter with 81% of the fibres smaller than 1 μ . No photographs of the rabbit nerve are given and no fibre size distribution is described. There is obvious muddling of the scales in the photographs presented (his fig. 12 & 13) and the mouse red cells present appear to be half their normal size. The distribution described by Yuri matches that above if the dimensions are doubled. The ratio of the fastest conduction velocity to the largest fibre diameter is 20 from his data which is quite outside the usual range of values. The fact that the present total count is in agreement with that of Bruesch and Arey (1942) is further support for the measurements of fibre diameter given above because the calculation involves the use of an area measurement made independent of the EM.

Correlation of the retinal ganglion cell diameter, optic nerve axon diameter and conduction velocity distributions is not possible at present for the unimodal curves described above.

Normalisation and superimposition of the high resolution retinal ganglion cell and axon diameter distributions simply indicates that the peak of the former lies half way along the scale while that of the latter is only 17% of the way. Similarly, Schade and Van Harreveld (1961) found themselves unable to identify two populations of cells in the cat peroneus tibialis motoneuron pool which showed the obvious difference in size distribution found amongst the α and γ fibres of the efferent nerve. No relation between cell and axon diameter appears to have been pragmatically determined for any population. An attempt at the theoretical derivation of the relation would be an amusing but, considering the complexity of the factors involved, a most probably unprofitable task. The curves are not related by the simple law /

law cell volume / axon cross sectional area = constant. There is, moreover, no reason to assume that only one diameter of axon is possible for a given cell diameter.

The correlation of conduction velocity and axon diameter is a much more theoretically approachable problem but an examination of the literature indicates that little success has been achieved. Recent counts of the diameter distribution for the rat (Forrester, 1967), cat (Bishop and Clare, 1955; Donovan, 1967), monkey (Ogden and Muller, 1966) and human (Chako, 1948) reveal distributions with peaks at 0.9, 1.5, 1.2, 1.25 and 1.2 microns respectively. In all cases, as in the rabbit, the distributions were unimodal. In contrast, the compound action potential of the optic nerve of all species studied shows a multimodal form. In view of the uniformity of the fibre diameter spectrum throughout the optic nerve of the rabbit and monkey (Ogden and Muller, 1966) it is not likely that the difference can be accounted for by preferential stimulation of certain groups by virtue of their position in the nerve. Other factors dependent upon the stimulating techniques used to elicit the compound action potential may well, however, influence its form.

An alternative explanation of the difference in form of the compound action potential and the axon diameter distribution arises from the work of Boyd (1965). It was shown that the assumption of a constant value of 6 for the ratio between the conduction velocity and diameter of axons in the mammalian peripheral nerve (Horsfall, 1939) is erroneous. In the peripheral motor nerve of the cat, the ratio is 5.9 for the alpha fibres, 5.0 for the fast gamma fibres and 5.2 for the slow gamma fibres. A population of optic nerve fibres which included groups with different ratios of conduction velocity to diameter would not give a unimodal compound action potential if the fibre diameter spectrum had that form. In the cat, the ratio is found to be different for the slowest and fastest fibres of the optic nerve. Bishop (1953) gives values of 8 and 14 respectively while Chang (1950) quotes 6.6 and 11.0 so that the above explanation would apply. The ratio is 10 for both ends of the rabbit distribution but this does not necessarily imply a constant /

constant value in the intermediate range. Further consideration of the literature would be pointless; more sophisticated investigative techniques are required.




Fig. 39 Optic nerve fibres of the nerve core showing broken down myelin sheaths. E.M. magnification about 6,000.

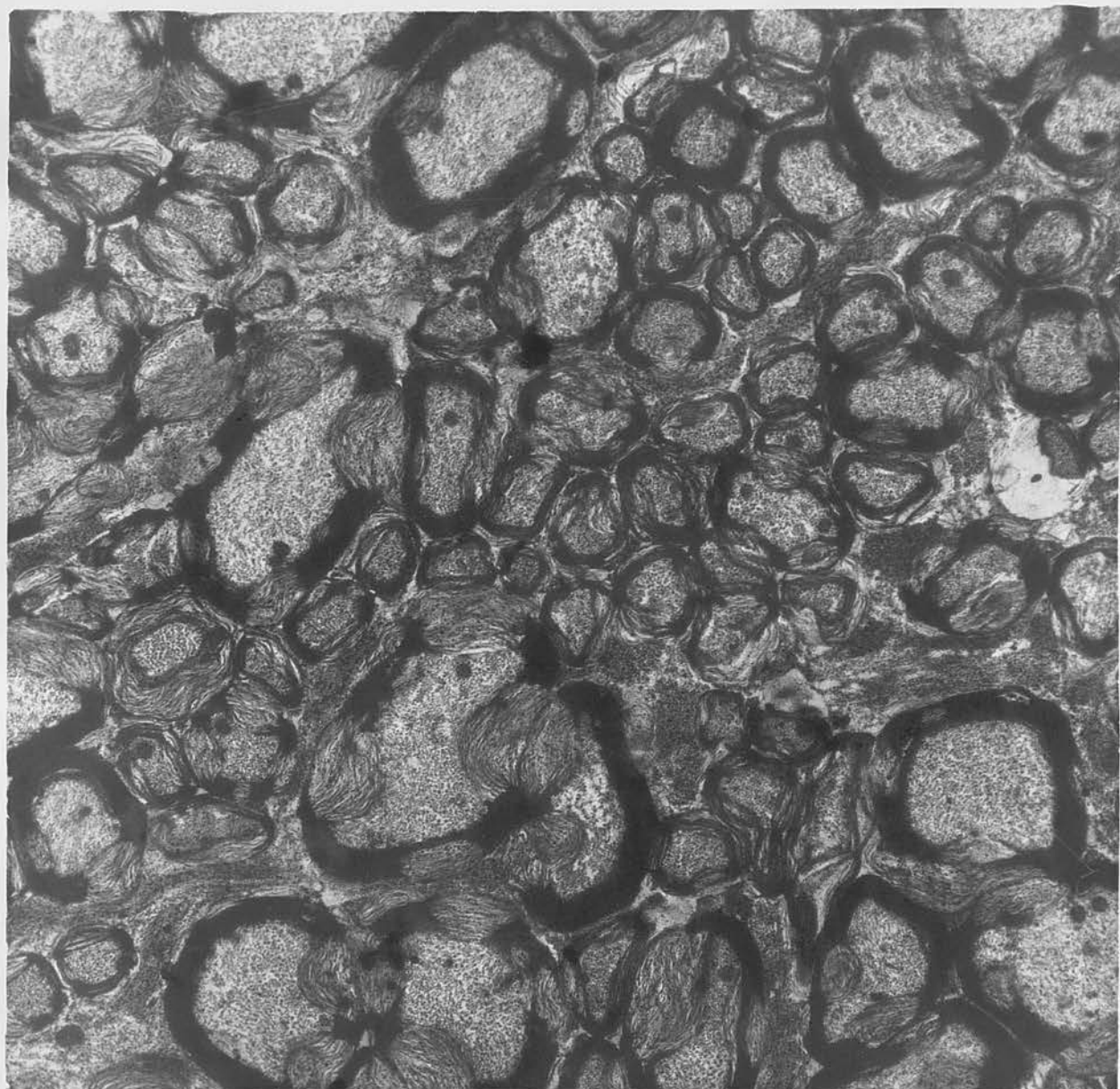


Fig. 40 More peripheral optic nerve fibres in a well preserved state.
E.M. magnification 6,000.

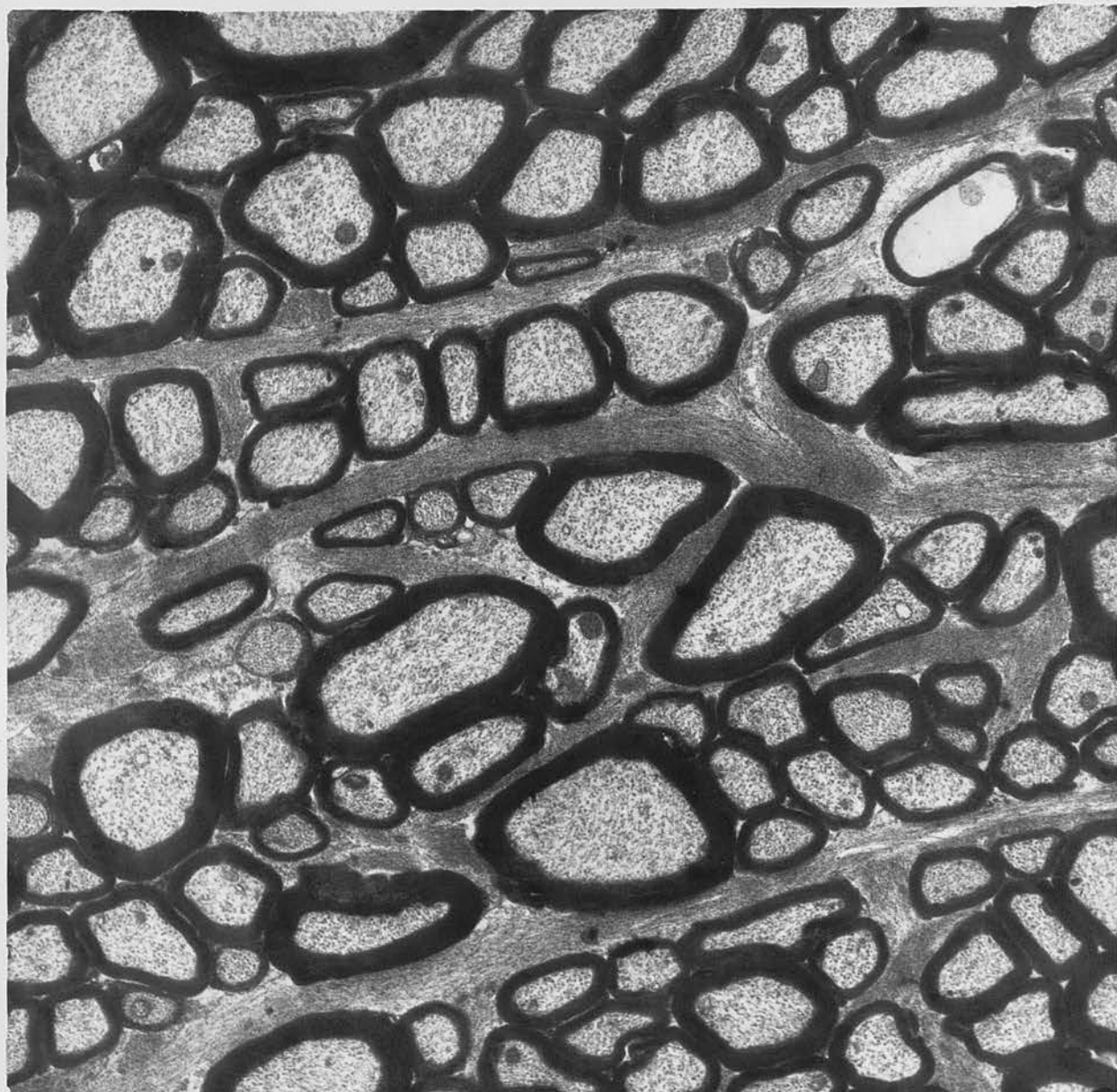


Fig. 41 Section through entire optic nerve showing 'core' of less well preserved axons. Magnification 110.

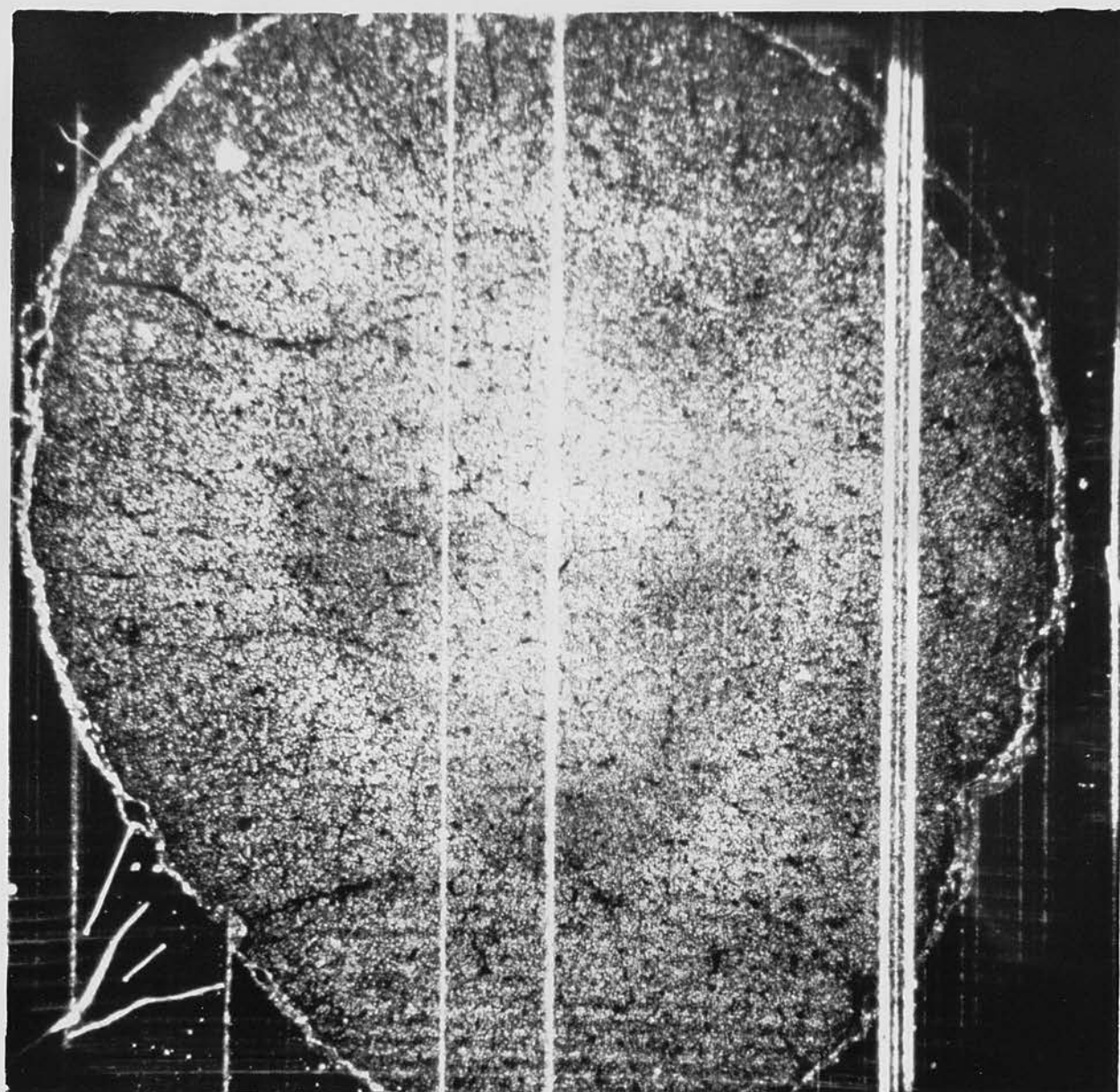
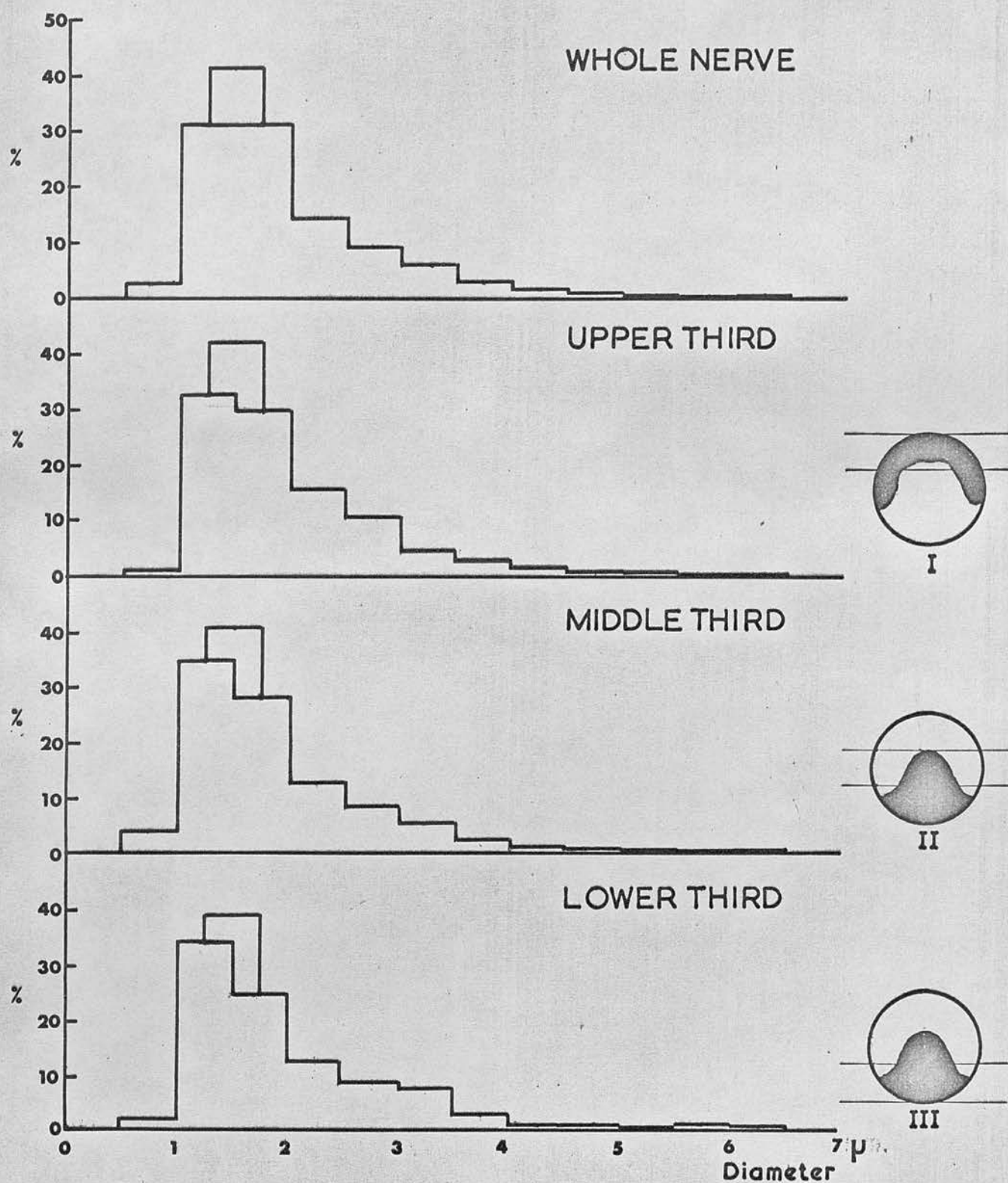


Fig. 42 Histogram of distribution of rabbit optic nerve axon diameters in classes separated by 0.5μ . The results are expressed as a percentage of the total sample counted in each case. Histograms are presented for whole nerve, upper third, middle third and lower third. The inserts show the degeneration patterns in the optic nerve of the rabbit subsequent to lesions of the whole upper retina, I, and both lower quadrants II, after Brouwer et al. (1923). The superimposed lines show the region from which the samples were taken for counting in each case. The samples are very similar in their distributions in all three regions.



OPTIC NERVE SINGLE UNITS

The examination of rabbit optic nerve single units was initially undertaken in order to study the directional units reported by Barlow et al. (1964) as present in the rabbit retina. The investigation was later extended in order to attempt confirmation of their other findings. In view of the small amount of literature dealing with units of the rabbit visual system, it was felt that the comparison of my findings in the optic nerve with those of Barlow et al (1964) would provide a useful test of the techniques employed below for the examination of single unit properties in other areas of the rabbit visual system.

METHODS

Two hundred and thirty optic nerve units have been examined in various degrees of detail during experiments on fifteen rabbits. Preparation was similar to that described in the general methods section except in that the animal was trephined at the midline, slightly caudal to the line joining the supraorbital processes of the frontal bone, and decerebrated by suction. The operation and experiment were carried out under urethane anaesthesia. Brain tissue overlying the optic nerve was cleared by the use of a fine pipette attached to the suction apparatus. Great care was exercised in clearing the nerves in order that their vasculature was not damaged. According to Bishop (1933) the arterial supply of the optic nerve branches from the ophthalmic artery and eventually forms the multiple central arteries seen at the optic nerve head. The capillaries of the nerve apparently return their blood to small veins which run along the nerve, just within its sheath, in company with several small arteries which pass to the eyeball and form the ciliary vessels. Any damage to these veins or arteries may cause ischaemia in which case the nerve, unlike mammalian peripheral nerves, rapidly becomes inactive. The region of optic nerve exposed is about 1.5 mm. wide and 5 mm. long. The nerve is surrounded in the cranial cavity by the dura (25 μ), arachnoid (5 μ) and the pia (up to 40 μ). Recording from this region was carried out with glass micropipettes filled with Wood's metal and tipped with platinum black. It was necessary to tear open the sheaths of the nerve /

nerve with a pair of tungsten needles before inserting the electrode. This operation and the insertion were carried out under a dissecting microscope in order to avoid injury to the nerve vasculature.

The rabbit optic nerve contains a great deal of connective tissue which separates the fibres into bundles. It is necessary to move the electrode up and down a few times before the tip enters one of the bundles when single units suddenly appear. If the units are maximised it is possible to hold them for half an hour or more. The majority of the units are about 100 μ V in amplitude.

In some cases spontaneously active units were recorded and their fields located after a search, in other cases responses were elicited from silent units by means of cardboard figures moved about in the visual field of the animal. Units with maintained discharge are readily detected by movement of a black or white card which inhibits or excites their activity upon entering their receptive field if the background lighting is held at a level at which both on and off units with maintained activity are firing spontaneously. The receptive field of each unit was plotted on a sheet of paper in the stimulus plane and the sheets were then filed.

RESULTS

In the ensuing sections the receptive field of a unit is to be understood as the region of the stimulus plane from which the activity of the unit may be influenced by some form of visual stimulus. This definition of the receptive field indicates one of the major problems of single unit studies for nomenclature of the classes is necessarily based upon the stimuli used which may differ somewhat from one laboratory to another. The adequate stimulus for certain types has probably been determined and their properties are distinct enough to make classification easy. In other cases certain features may be picked out as typical of a class and yet be found in various intermediate forms. The group of concentric units described below are of such a variegated form. The subclasses listed are approximate and exclusive so /

so that the grouping might readily be changed by the discovery of a more appropriate stimulus or by a slight change in the experimental conditions.

The units of the optic nerve may be divided into concentric and non-concentric types. The latter group consists, in these results, of the adjacent on-off type alone. The concentric units all reveal a centre surround organisation but various techniques are required to bring this out. On, off and on-off centres have been recorded. The on-off centre units have all shown directional properties. The on and off centre classes have been found to contain similar subgroups and no further distinction will be drawn between them although the relative proportions of the subgroups vary in each case. The attribution of a short descriptive and exclusive title to each of the subgroups of the on and off concentric class has proved difficult and a simple numerical classification has been resorted to which uses arabic numbers to avoid confusion with the frog classification.

Concentric Units.

1. (Small field, transient centre on or off response). These on or off centre units give a readily identifiable centrifugal or centripetal response respectively to the movement of a black 1° card disc through their field. The field centres mapped in this fashion are about $0.5-3.0^\circ$ in diameter. A small spot of light switched on and off elicits a transient response from the field centre (fig. 43a) but very rarely does so from the periphery. The presence of a surround may, however, be demonstrated by more powerful stimuli. An annulus projected on the periphery and turned on and off or constant illumination of the centre region accompanied by the switching of the background light are manoeuvres which will bring out the surround response in the opposite phase to the centre (fig. 43b). Another powerful means of investigating all the concentric types was obtained by projecting the image of an iris diaphragm aperture on to the field. Expansion of the diaphragm increases the illumination of the field and contraction reduces it. On regions of the field respond during expansion and off regions during contraction while the moving edge of the field provides a /

a powerful maintained stimulus. The points at which on firing and off firing begin may be noted and if differently placed indicate the extent of the on-off area. The method clearly delimits the extent of the surround, for this region responds well to moving edges, and is the only technique apart from arduous threshold plots by means of which the feat is possible. The introduction of a neutral density wedge enables the effect of different intensities of illumination on the centre surround organisation to be quantitatively investigated. The averaged results indicate centre diameters at spot intensity of 5×10^{-6} to be 2.2° for off units and 2.6° for on units. The surrounds measured by the expansion test (fig. 43c) were from 10° to 20° in diameter. These units respond to movement in the field but do not fire in response to shadow or fast moving stimuli ($100^\circ/\text{sec.}$).

2. (Dark adapting off units). Only off centre units have been found in this class. When the field centre is plotted by the movement of a card against an illuminated background or with a light spot under the same conditions it is found to be small (0.5° to 1.0°). Mapping with a spot in the dark demonstrates a considerable increase in size of the field centre. The effect does not result from the increased contrast alone for the expansion test shows a similar change of surround to centre response when the illumination of the expanding spot is reduced one hundredfold. The phenomenon is similar to that occurring in the receptive fields of the cat retina during dark adaptation but develops much more rapidly. The change in organisation can be demonstrated in the time required to slide the neutral density wedge to its new position if the expansion test is used. Under normal background illumination the presence of a surround may be demonstrated. Some of the units show a little spontaneous activity in the dark and are able to follow fast movements. The response to the turning on and off of the stimulus spot is transient.

It is possible that the next two classes form a continuum. The difference in their performance may not appear to depend upon much else than the presence of maintained firing in one case and not in the other. During an /

an experimental investigation, however, the units have a quite different 'feel'. Maintained and non-maintained units have been recorded simultaneously and immediately after one another so that even if the level of activity is a function of the anaesthetic depth it would appear that the population reflects some inhomogeneity in its sensitivity to drugs.

3. (Concentric maintained units). These units all show maintained firing in the dark or light and some show activity under both conditions. The on and off centre types have similar properties. The most characteristic units show a change in timing rate which has been observed to continue unaltered for some 15 minutes when a light spot is switched on or off in the receptive field but the response ^{starts with} is ~~initiated~~ by a short higher frequency transient burst. Other units show much more transient response which adapts rapidly to some lower maintained firing level which is a function of the light intensity.

Figures 44a, b show maintained firing when first the centre and then the surround and centre are illuminated at an intensity of 10 lux . Note the marked reduction in maintained firing when the surround is brought in. If the centre is illuminated alone at intensities differing by a factor of one hundred in intensity then the firing frequency is by no means so markedly reduced (fig. 44c,d). The maintained centre response is thus accompanied in these units by a maintained inhibition from the surround. At low levels of illumination the pure centre response can be obtained from a suitable sized spot but the surround comes in if the diameter is increased (fig. 44e,f). At higher intensities of illumination a spot covering the centre of the off unit in figure 45a elicits an off response but on the return of illumination the firing is first inhibited and then followed by a short burst of two or three spikes after which the maintained activity returns and takes some time to die away. Inclusion of the surround within the illuminated region brings about the rapid cessation of ^{maintained} firing at on of the light (fig. 45b). The prolonged firing at on when the centre is illuminated thus appears not to be an on response but a carrying over of the activity of the off period. The on response /

response manifests itself in the inhibition and short burst. In many cases it was noted that the magnitude of the short burst obtained in transferring from the maintained to non-maintained firing state is dependant upon the previous duration of the maintained firing. Fig. 45d shows that the on response of an off unit contains four spikes after 0.5 sec. maintained firing, and one spike after two seconds. The elucidation of these centre surround phenomena is a pressing problem but cannot be undertaken satisfactorily with these techniques as the centre and surround as mapped out above are only the manifestations of interaction between completely overlapping and probably similar sized excitatory and inhibitory receptive fields (Wagner & McNichols, 1963). These fields cannot be separately stimulated unless they have different spectral sensitivities as is the case in the goldfish retinal units described by the above authors.

The maintained units are able to follow the fastest movements that could be presented by hand which are in the order of 300° per second. Figure 46a shows the grouping of the spikes which occurs when first a pencil and then a hand is moved through the illuminated receptive field marked on the projection screen.

The maintained firing may be modulated from either centre or surround. The on unit of fig. 46b is firing in maintained fashion in response to a white 3° disc in the receptive field centre while the remainder of the background is black. The movement of another white (5°) disc into the periphery exercises a considerable and maintained effect on the firing rate. The surround inhibitory effect can follow rapid movements as is seen in fig. 46c. Marked maintained inhibition could be obtained up to about 10° from the field centre but moving stimuli were effective at modulating the activity when 25° away from the centre in some cases.

The firing rate of maintained units varies over a wide but variable range of illumination. If the intensity is changed in small steps then firing is momentarily inhibited or the spikes group together to form small bursts depending upon the nature of the unit and the direction of the illumination change /

change. The effect is not as marked as for the next class (fig 46d,e).

Class 3 maintained units show an average centre diameter of 2.8° for the off units and 3.2° for the on in observations made during the application of the expansion test.

4. (Large field, shadow sensitive units). This group contains units with low levels of maintained activity, slowly adapting or rapidly adapting responses. Figure 47a shows the response of a [redacted] a rapidly adapting on unit to the flashing of a 1° spot in the field centre. Figure 47b shows the more massive response of the off unit when the spot is enlarged to take in the whole of the field centre but not the surround region. In figure 47c the spot is enlarged even more and the surround introduced. When this occurs the response, which is monitored through an audio amplifier and speaker, sounds distinctly oscillatory as if the surround and centre are alternately coming to dominate the ganglion cell output. The effect is most pronounced with intermediate states of surround illumination and does not sound so marked when the whole field is stimulated (fig. 47d). Examination of the photographs shows the rhythmic change from firing to inhibition and the appearance of a marked on effect when the surround proper is illuminated.

The centre and surround of these units will often both respond to the flashing of a small stimulus spot. The centre mapped in this fashion is usually about 4° in diameter while including the surround the field approaches 8° across. The junction of centre and surround often consists of an on-off zone. The response to the expansion test is vigorous from centre and surround (fig. 47e) and the regions show overlap. The average centre diameter as estimated by this test is 4.2° . The surrounds can be activated within a 20° diameter circle. Search for these units is often difficult if carried out with black cards held in the stimulus plane against a white background, but the shadows of these cards held in the beam of the background illumination projector are most effective stimuli. Small objects or the faintest of shadows are also very good stimuli. The movement sensitivity is very /

very great and firing in response to stimuli is grouped. The audio monitor consequently generates a rather squeaky sound during their response and this, along with the sensitivity to shadow and the much lower level of maintained firing, if present, serve to distinguish the class 4 from the class 3 unit. On and off types have been observed but the latter form the largest population.

The class 4 unit will respond to very small decrements or increments (depending on whether off or on type) in the field illumination (fig. 48a,b). The response is almost equally vigorous to centre and whole field illumination. The bursts in fig. 48a,b are each responses to about 2-3% change in the illumination level. The sensitivity of these units is much more marked than that of the maintained type. The lower firing rate releases more of the dynamic range of the unit for the generation of the response which does not vary much in its strength at each end of the illumination scale.

These units respond similarly to rapidly moving stimuli presented either to the centre or to centre and surround. The units follow the fastest movements that can be generated by hand (300° sec.), (fig. 48c). The response to slowly moving stimuli may also be good. Records have been obtained of units responding to the movement of an edge across the field at from 60° to 0.1° per sec.

The distinctive properties of the class suggest some special 'alarm' function (Barlow et al., 1964). In a subsequent section it will be shown that these units reach the colliculus and that the above interpretation of their function is most probably correct.

5. (Directional unit). All of the directional units gave on-off responses throughout the region responding to an exploring light spot. Figures 49a,b,c show the response of a directional unit at on and off of a 1°, 2° and 4° light spot centred on the field. The effect of a lateral inhibitory surround is apparent in the last case although the extent of the inhibition is not great enough to eliminate the response to the passage of a projected grating of 2° wide by about 50° long bars through the receptive field (fig. 49d). The latter figure shows the directional property of the unit /

unit. The projected grating bars are first swung nasal to temporal and the photocell in the field indicates their passage on the monitor trace. When the grating is swung in the opposite direction, a smaller unit responds but the directional unit does not. The directional unit will fire in response to movement of large or small objects along the field radii over a sector of about 270° . Movement into the field over the remaining 90° sector did not initiate a response unless the velocity was extremely low. The directional sensitivity was unchanged whether black stimuli were presented on a white background or vice versa so that the response of the unit is not simply dependant upon the arrangement of on and off regions within the field. Figures 49e, 50a, b show the response of a directional unit to 1° , 5° and 25° long by 1° wide bar passing in the preferred direction through the field at constant velocity ($60^\circ/\text{sec.}$). The degree of lateral inhibition may be seen in the decline of the response to the longest bar.

A qualitative demonstration of the directional response is given in figure 50c. A black card is moved first through the field in the null direction and passes over a photocell on each side of the field in turn giving rise to two steps in the monitor trace. On its return along the same path the edge elicits a response from the unit. In figure 50d the arrangement is similar but the movement is along an axis perpendicular to the former path and firing is elicited in both directions. The response in the preferred direction of stimulation was present over a range of velocity from 150° sec. to less than 0.5° sec. (fig. 50e, 51a, b, c, d). Firing in the null direction appeared at the lowest rates of movement in the order of 0.5° sec. (fig. 51e).

Non-concentric

6. (Adjacent on and off unit). These units were quite rare. Responses could be obtained to the movement of a black disc or bar along, in some cases, a horizontal axis or, in other cases, along a vertical axis. No response could be obtained to movement along the axis perpendicular to that from which a response was obtained unless the card was displaced to one side or

or the other of the axis. In the latter case a centripetal response would be obtained from one side and a centrifugal response from the other. The field thus consisted of an on and an off region adjacent to each other and exercising mutual inhibition. A black card moved first over the off region and then over the on produced a biphasic response while movement in the opposite direction generated only one burst of firing. The card passing along an axis at right angles to this stimulated both regions if properly centred and inhibition eliminated the overt response while if the card was not properly centred, it stimulated only one region of the field. The field could be mapped out with a light spot.

Figure 52a shows the response of such a unit to a white 3° disc moving, against a black background, into the on field and causing firing. In fig. 52b the firing is produced only upon exit from the off field. The maintained nature of the reciprocal inhibition exerted between the fields is shown in fig. 52c. A white 3° disc was placed in the off field. A similar disc was moved, still against the black background, in and out of the on field. The movement is indicated but no response was obtained. Removal of the white disc from the off field produces a burst of firing as the black background is revealed and the response of the on field is once again (52d) demonstrated. The response of the on region is potentiated by 2 minutes of inhibition from the off region (fig. 52e) and the potentiated response slowly returns to normal upon repeated presentation of the stimulus to the on area after the removal of the white card from the off region. The fields were about 2° by 4° along their minor and major axes.

7. (Giant field). Only two units in this class have been recorded. The receptive field of the unit appeared to consist of the entire visual field of the eye. The unit responded to the off of a 5° spot flashed anywhere in the field although the threshold for the response was lower along the horizontal. The increase of the spot to about 8° in diameter changed the response to on-off at all points stimulated. The constancy of this phenomenon coupled with the similarity of the threshold at the most nasal and temporal regions of the field contraindicates light scatter as an explanation of the size of the receptive field.

TABLE: NUMBER AND PERCENTAGE OF VARIOUS
CLASSES OF OPTIC NERVE UNIT

		Class	Description	No.	%	
CONCENTRIC	ON	1	Small field transient	36	15.6	
		3	Maintained	29	12.6	<u>ON</u> 32.6%
		4	Large field shadows	10	4.4	
	OFF	1	Small field transient	48	21.0	
		2	Dark adapting	39	3.9	
		3	Maintained	30	13.0	<u>OFF</u> 55.7%
		4	Large field shadows	41	17.8	
	ON OFF	5	Directional	21	9.1	9.1%
	NON CONCENTRIC	6	On and off adjacent	4	1.7	1.7%
		7	Giant field	2	0.9	0.9%
				230	100%	

Figs 43 - 52 Optic nerve unit responses which are described on pages 51-58.

General Notes on Photographs of Single Unit Responses

- (a) All pictures contain a time mark trace showing 100 msec. pulses.
- (b) Monitor trace

(i) If the corners of steps in the trace are rounded in records of responses to on-off flashes of light then the monitor trace indicates the output of a photocell placed within the path of the light beam providing the stimulus. Monitoring of stimuli entering and leaving the receptive field of units or of step intensity changes, dimming and brightening tests, are also carried out by means of photocells.

In all these cases, off of the light is indicated by a downward movement of the trace, unless a black spot is to be found on the right of the page number when off is indicated by upward movement of the trace.

(ii) If the corners of steps in the monitor trace are very square then the trace indicates shutter operation; in these cases up steps indicate opening or closing of the shutter. Down steps indicate resetting of the shutter and should be ignored. No absolute indication of on or off of the light is given but phase of the intensity change indicated will be readily ascertained from the accompanying text.

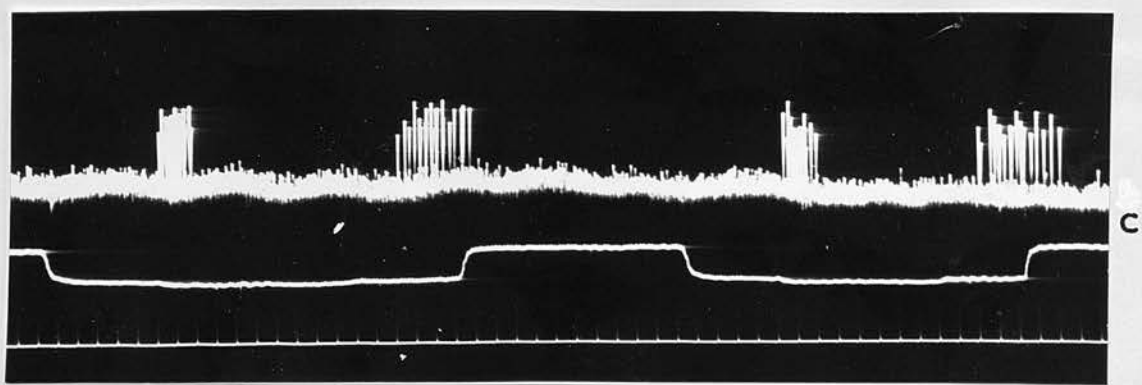
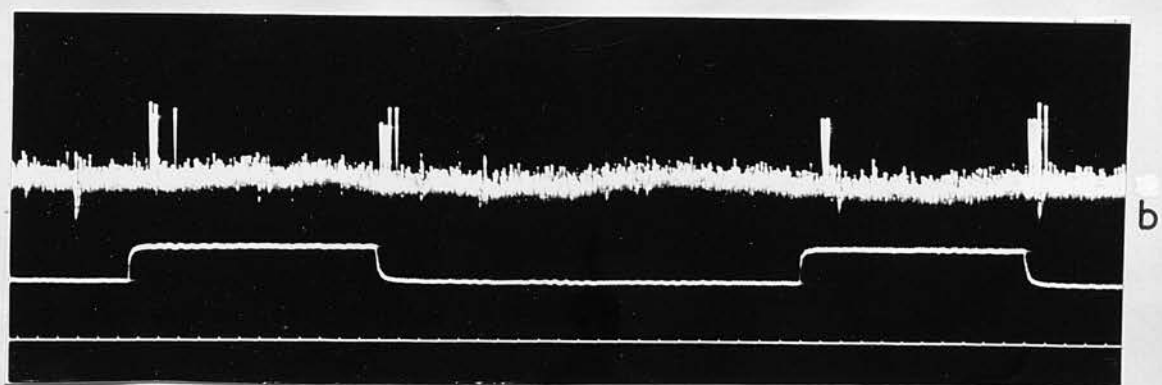
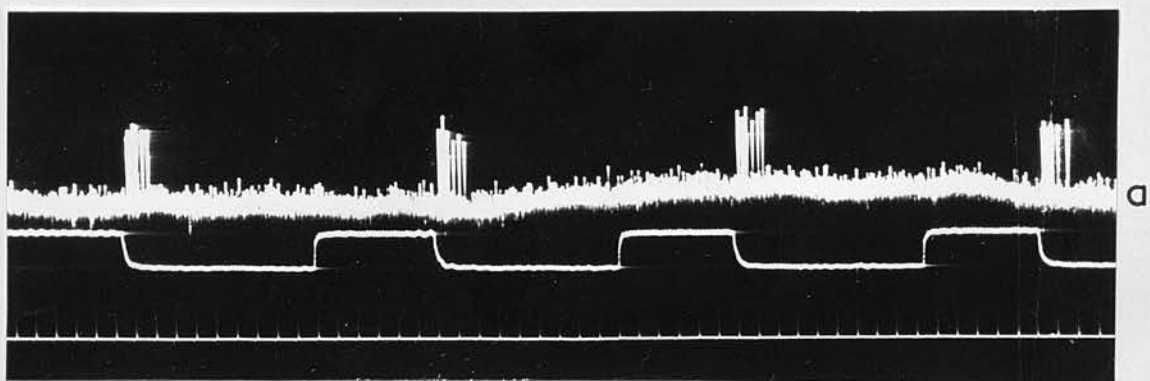
(iii) The expanding spot test was carried out with one photocell set in the stimulus plane at the edge of the receptive field centre and another at the boundary of the periphery. The first step up in the monitor trace indicates the spot has expanded beyond the receptive field centre, the second that it has expanded beyond the periphery of the field surround. The first step down indicates entry of the spot boundary into the peripheral receptive field and the second down that the spot has contracted into the field centre.

(iv) Stimuli moving at constant velocity which have been produced by the visual stimulator (page 262) are shown to be entering the receptive field by a downward movement of the monitor trace at a rate proportional to the stimulus movement velocity. The return sweep, if present, is to be ignored. Photocells were usually placed in the path of the stimulus on each side of the receptive field so that the region of the trace which is contained between two bumps indicates the period during which the stimulus was within the receptive field.

Off unit. 1° spot flashed at centre. Off at down
of monitor trace.

Off unit. Centre under constant illumination but
background flashed . Surround response at on is
evident. Off at down of monitor trace.

Off unit. Expansion test showing response to expansion of
light spot through surround and constriction through centre.
See page 52.



On maintained unit. Centre illuminated at 100 lux.

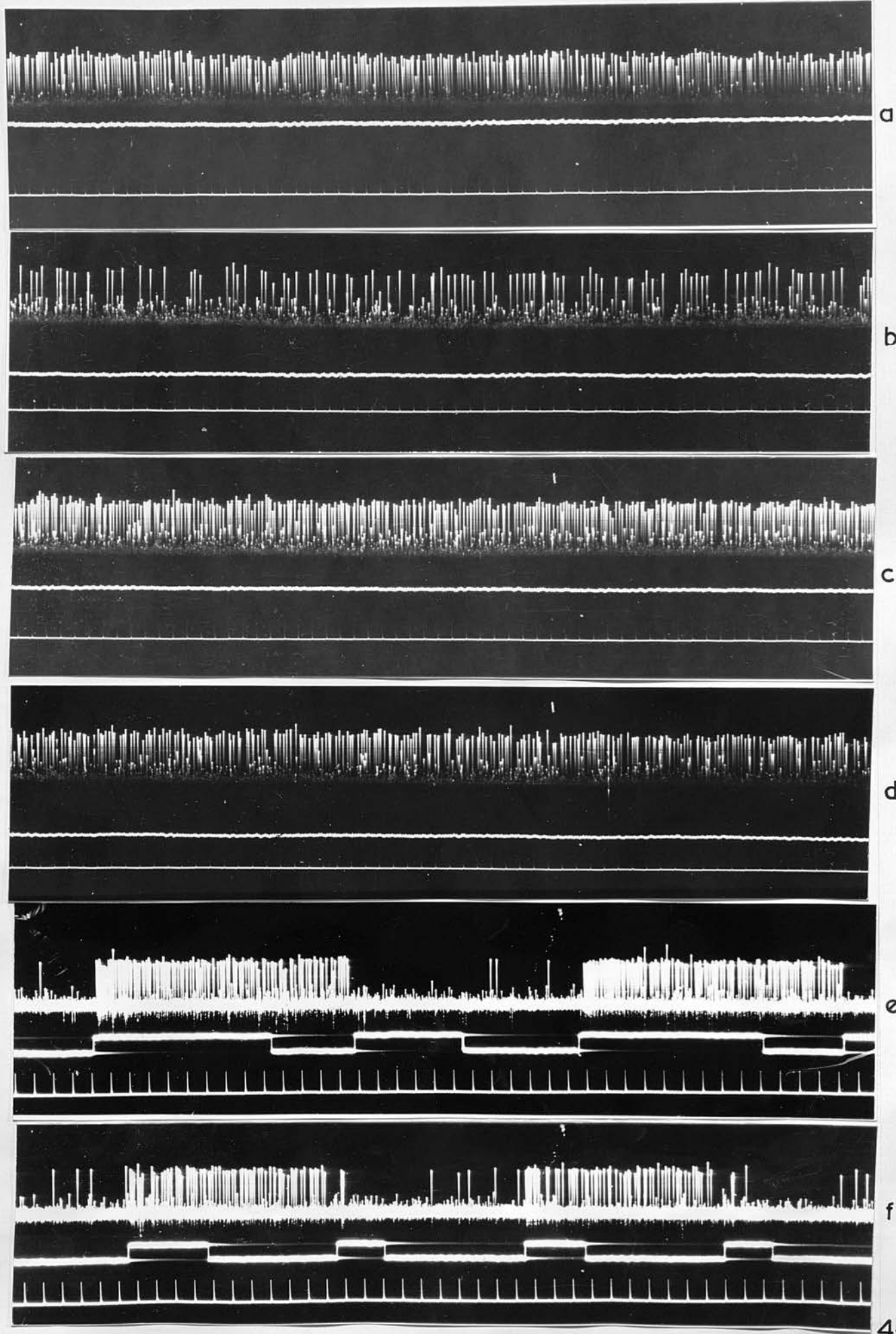
On maintained unit. Surround brought in .

On maintained unit. Centre illuminated at 10 lux

On maintained unit. Centre illuminated at 1 lux.

1° spot on centre at 1 lux. Ignore monitor downstrokes;
up is on , off, on etc.

3° spot at 1 lux. Monitor as above.



Off unit with 1° spot illuminating centre . Firing is maintained in dark with short burst at on of light followed by prolongation of maintained activity for a short time. Ignore down strokes of monitor trace; up is off, on, off etc.

Increase of spot to 3° in diameter inhibits prolonged maintained firing leaving short on response .

Off unit showing 2 spikes at on after 0.5 sec in dark. Monitor as above.

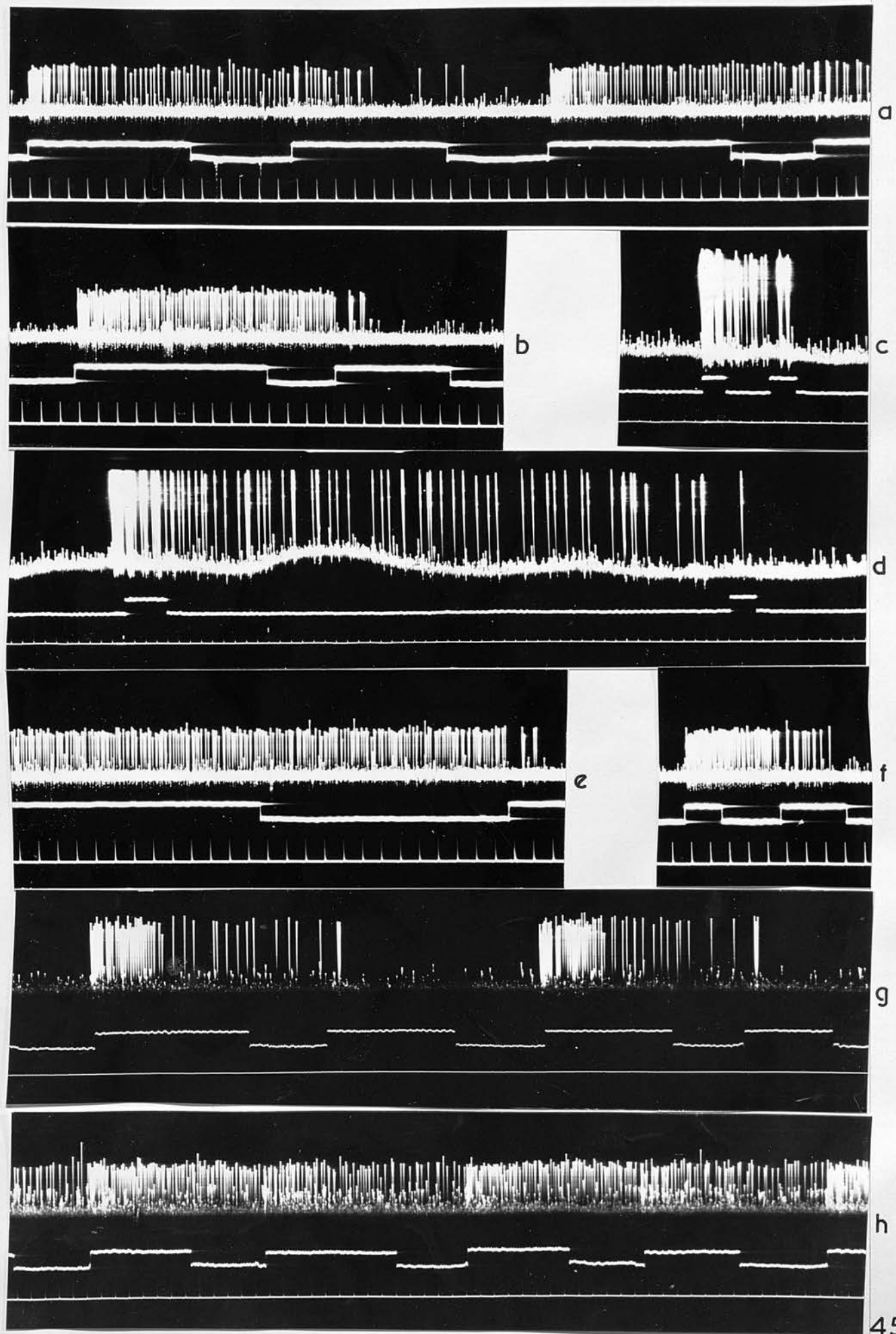
Off unit showing 1 spike at on after 6 sec. in dark. Monitor as above.

Off unit with 3° spot of light centred on field. 3 sec. in dark then light flashed at up of monitor trace. 4 spikes in on response

Off unit . In dark for only 0.5 sec. on response contains eleven spikes . Ignore downstrokes; First up is off second is on of light spot.

Off unit . Quite rapidly adapting with short on response. Ignore monitor ~~downstrokes~~ . First upstroke is off, then on, off etc.

Off unit . Much less rapidly adapting than above. Monitor trace to be read in same fashion.



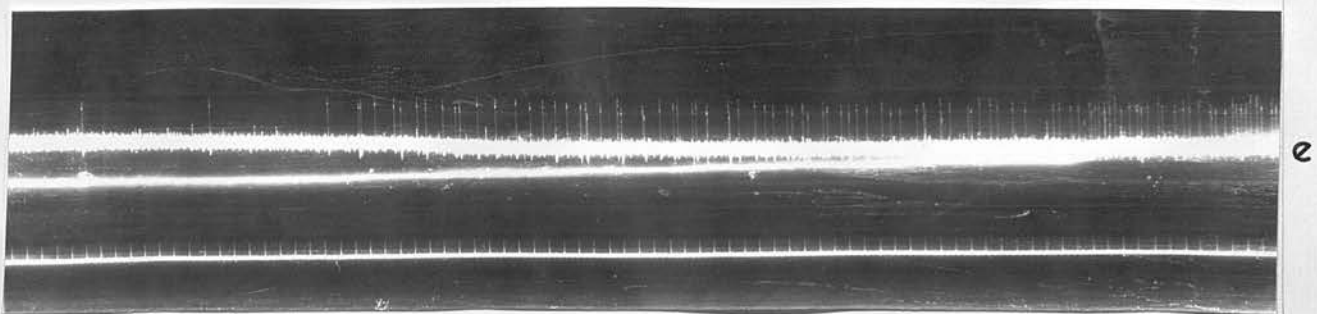
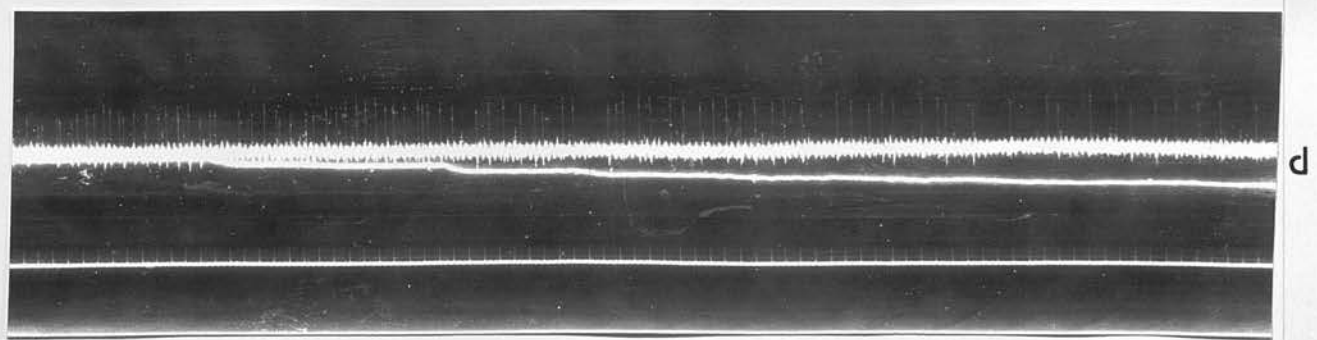
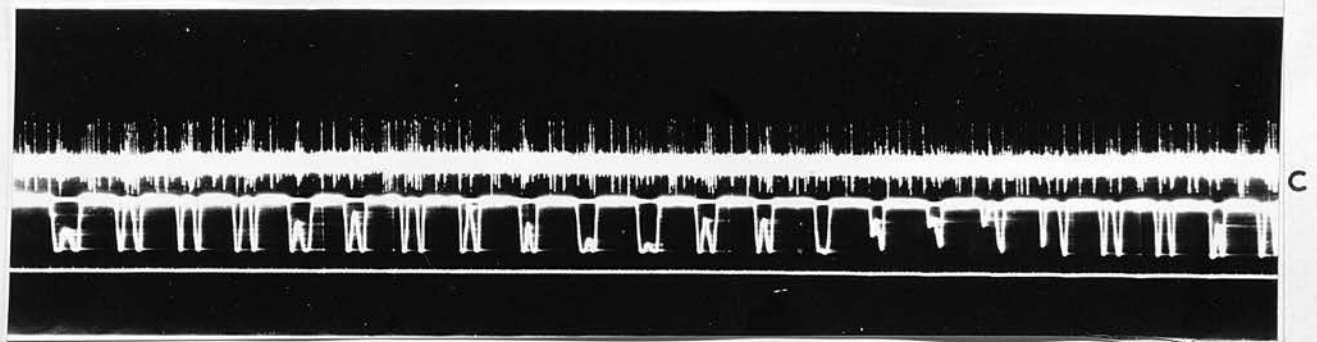
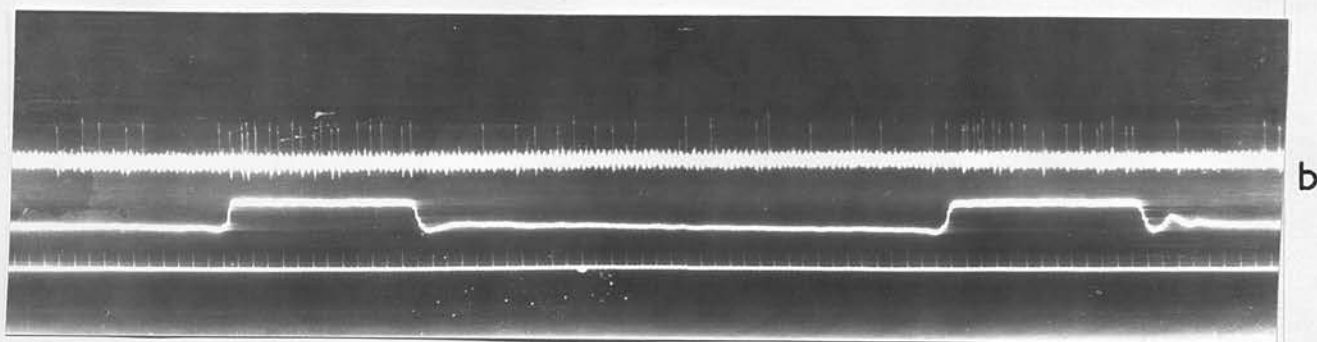
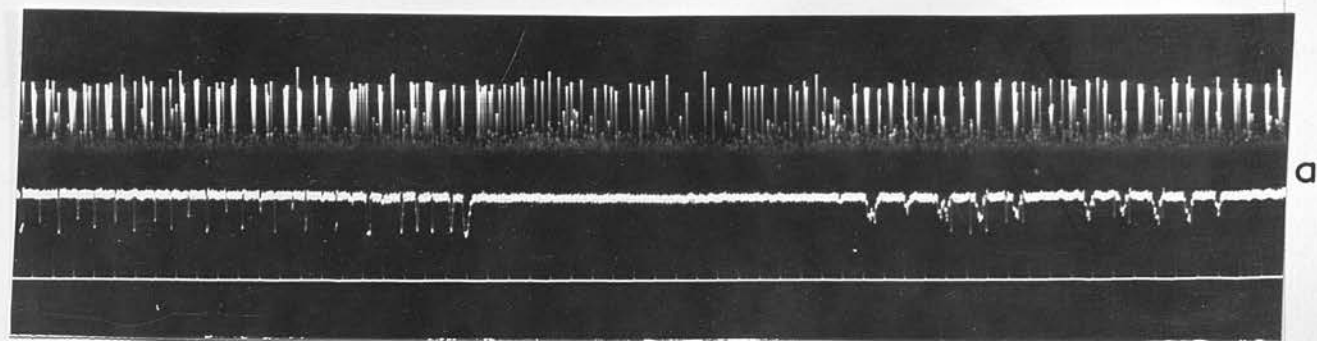
Maintained on unit . Firing in response to rapid movement of finger shadows in receptive field as monitored by lower trace.

On unit firing in maintained fashion to 3° white disc in field centre . Background black. Down of monitor trace indicates movement of 5° white disc into receptive field surround which causes inhibition of firing. Inhibition is maintained.

Maintained unit as above showing ability of surround inhibition to be elicited by rapid movement of the 5° disc.

Maintained on unit . 3° spot light intensity changed decrementally.

Maintained on unit . 3° spot light intensity changed incrementally. Monitor trace up with brightening.



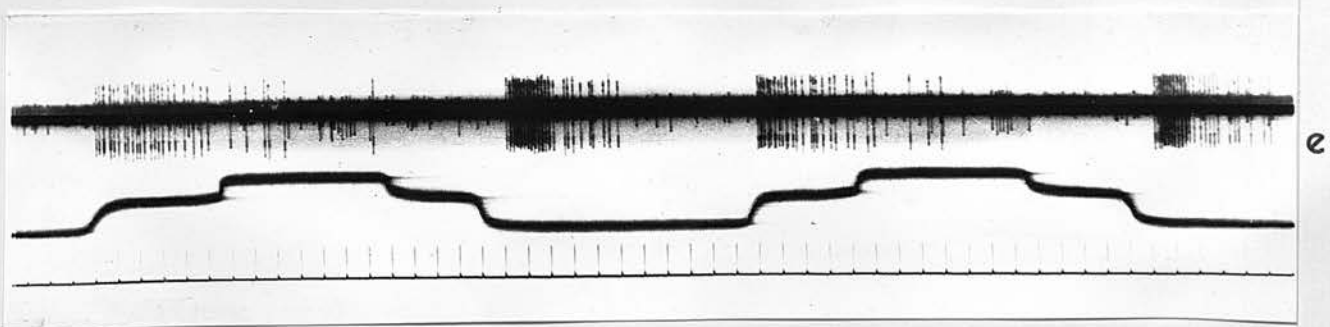
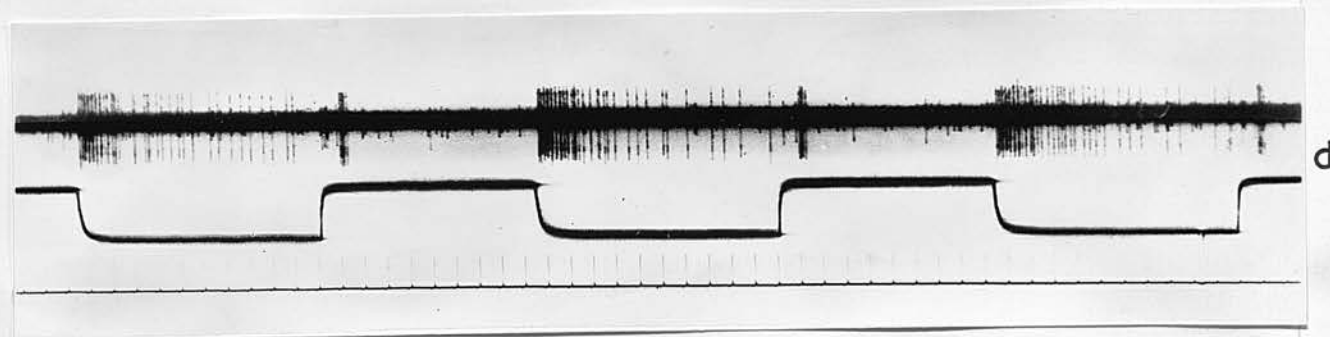
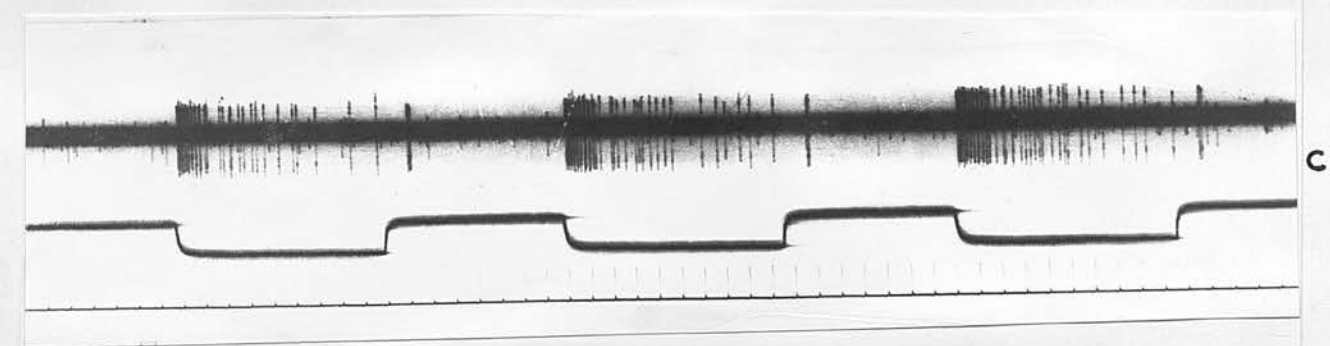
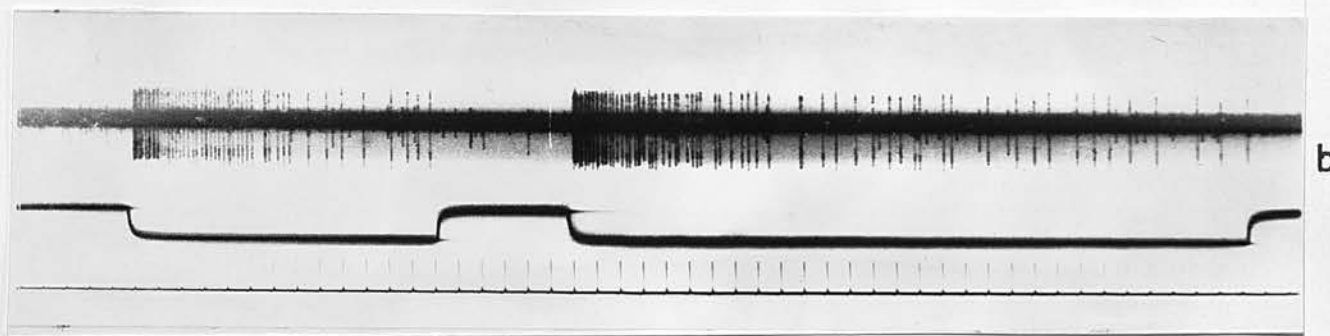
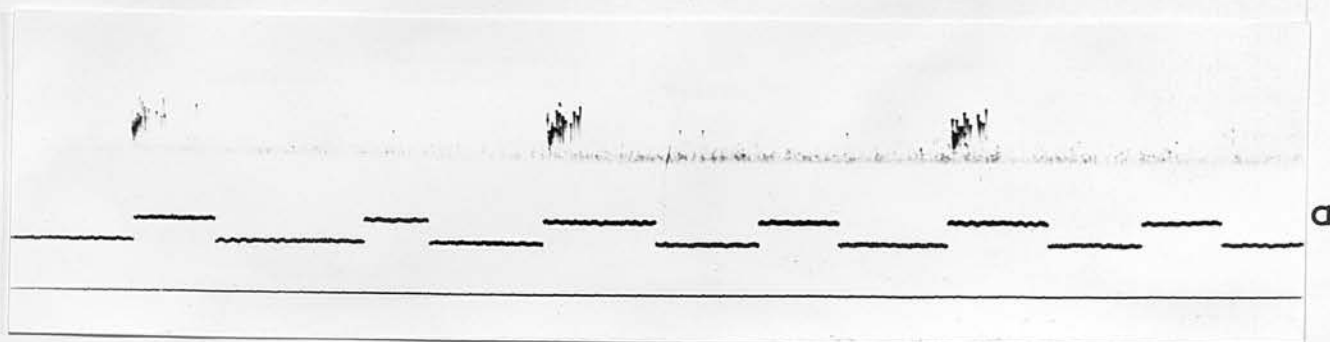
Rapidly adapting large field on unit. Ignore downstrokes of monitor trace. Upstrokes represent on , off , on etc of 1° light spot.

Large field off unit . 3° light spot flashed on centre only . Off is indicated as downward movement of the monitor trace.

Large field off unit. Flashing of a 5° spot . Monitor as above

Large field off unit. Whole field flashed . Monitor as above.

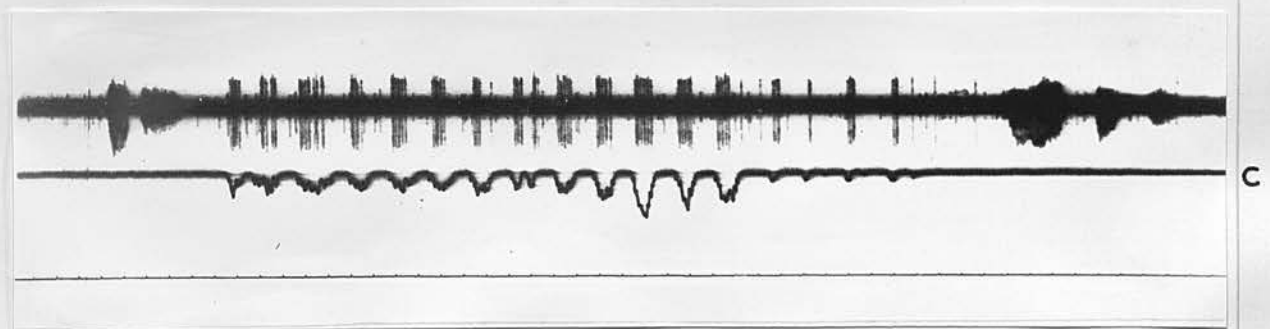
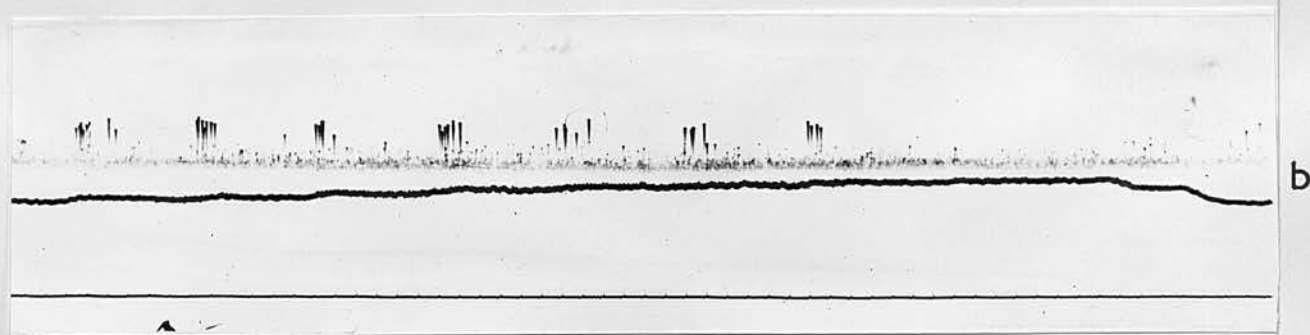
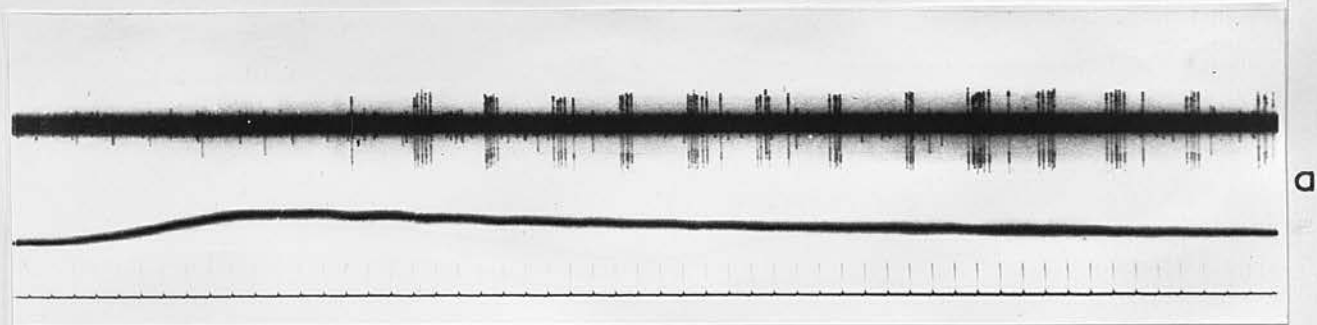
Large field off unit . Expansion test. (See note iii facing illustration 43). On response during expansion through surround. Off response during contraction of spot through centre.



Large field off unit. Centre illuminated by 1° spot . Monitor trace indicates brightening by up movement and darkening by down. Unit fires with burst to each decrement in intensity.

Large field on unit. Similar conditions to above but unit fires to increments in intensity.

Large field off unit firing in bursts to rapid movement of finger shadow through its receptive field as indicated by monitor trace downward movement .



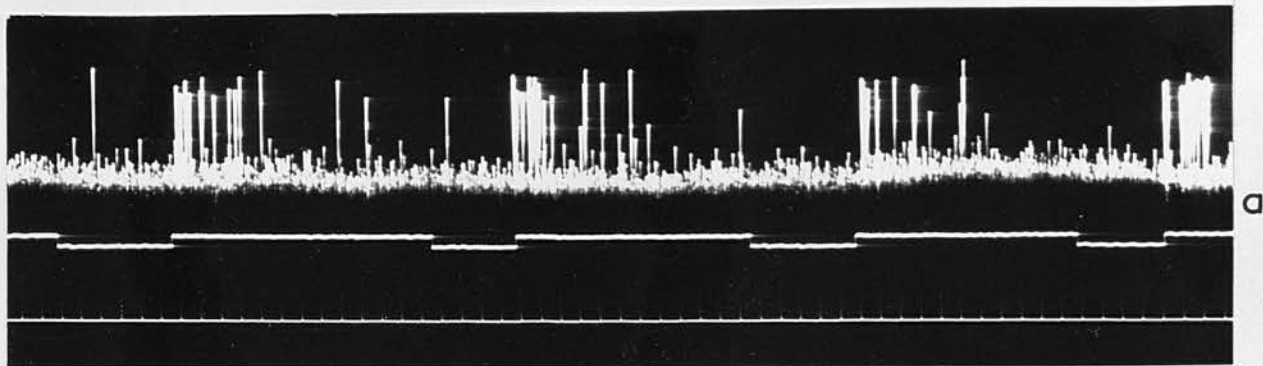
Directional unit. In this and subsequent pictures the downstrokes of the monitor trace must be ignored . The upstrokes indicate on , off , on etc. On and off response to 1° spot on centre of field.

Directional unit. Conditions as above but 2° light spot reduces response.

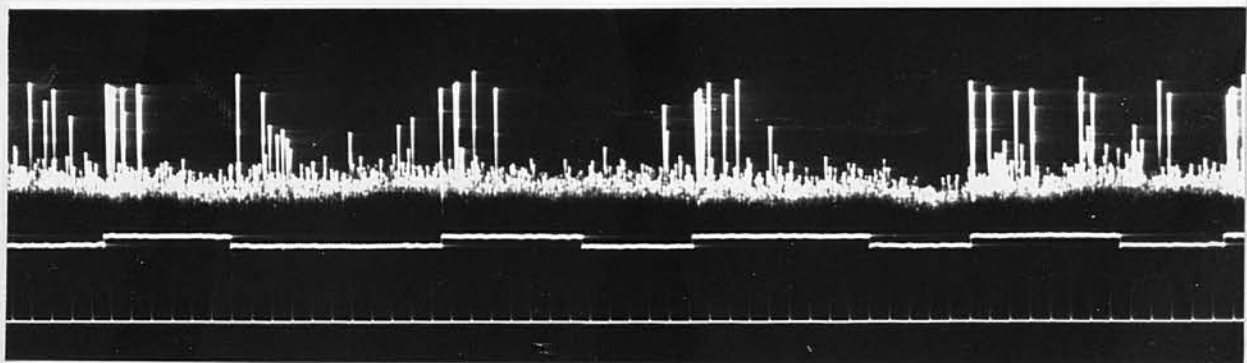
Directional unit. Conditions as above 4° light spot overlaps surround of unit . Response very weak.

Directional unit. Projected image of 2° period , black and white grating of bars about 50° long moved left to right and then right to left through field. Large, directional , unit action potential appears only in latter case . Monitor trace shows passage of grating image over photocell near receptive field . Lateral inhibition not very powerful.

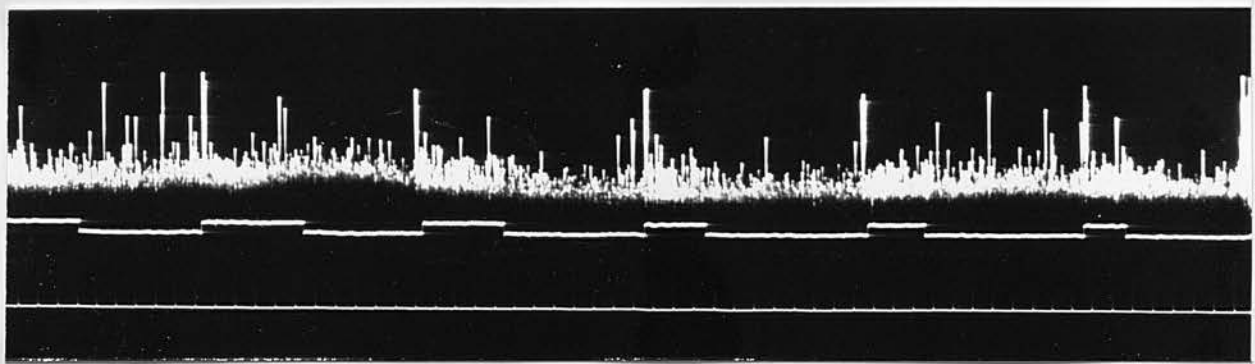
Directional unit. 1° wide bar of light passing in preferred direction through field at 60° /sec. Monitor trace downward movement indicates relevant portion of signal . Two bumps on gradient of monitor trace indicate passage of stimulus over photocells placed just outside receptive field on each side.



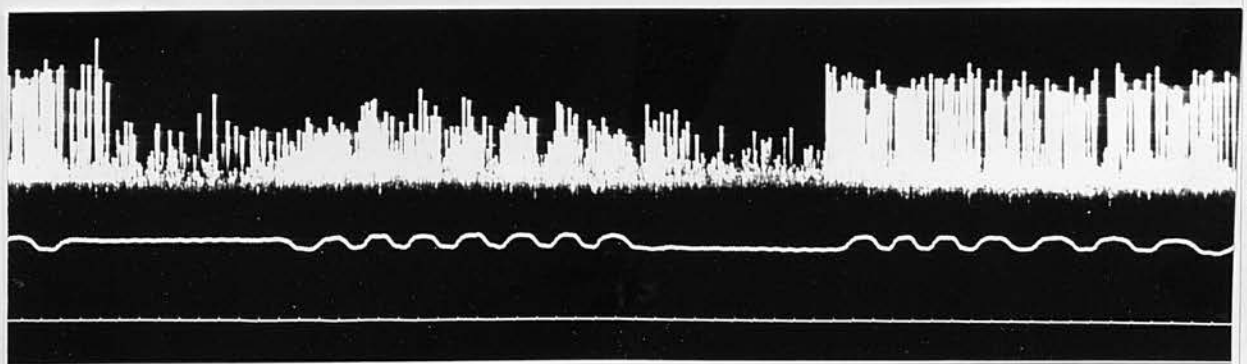
a



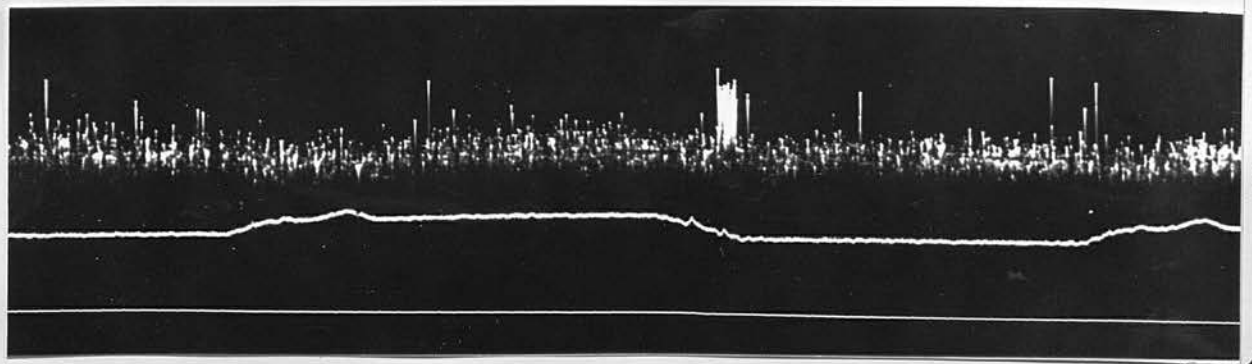
b



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d



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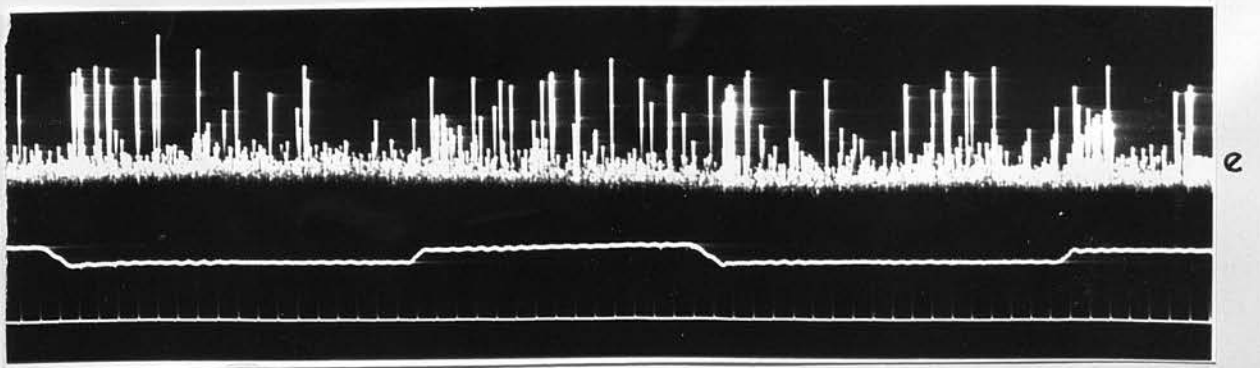
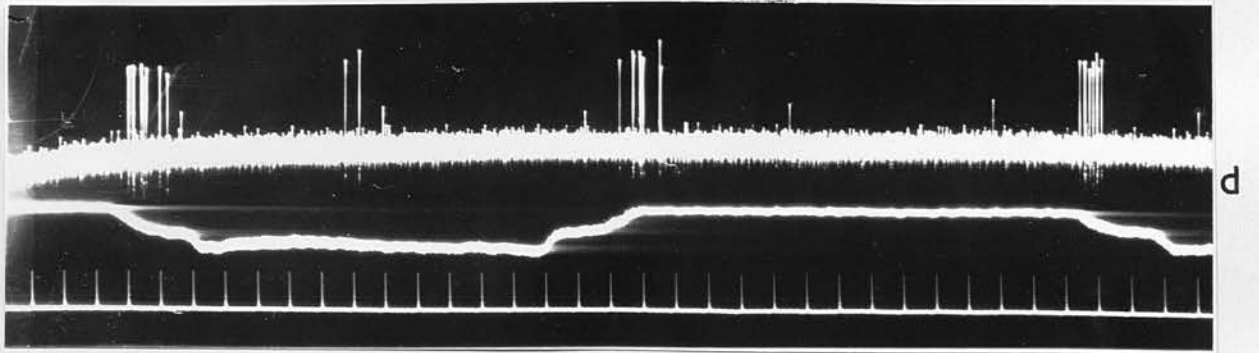
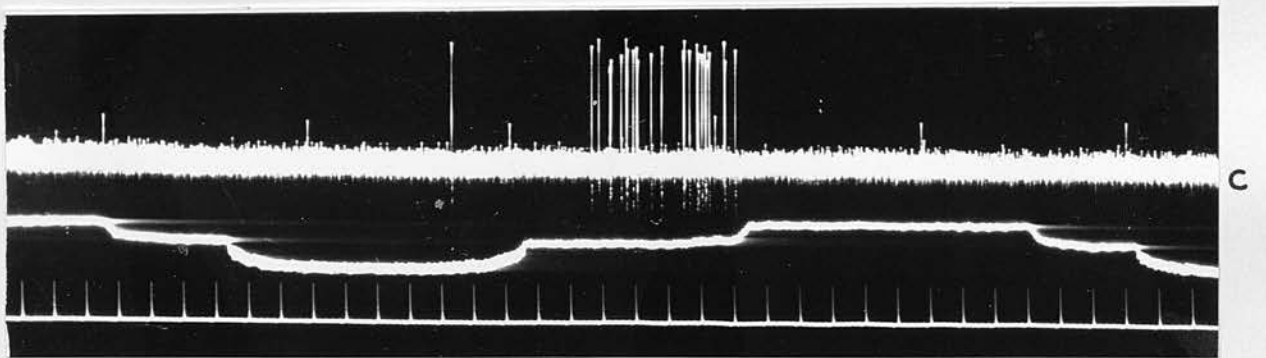
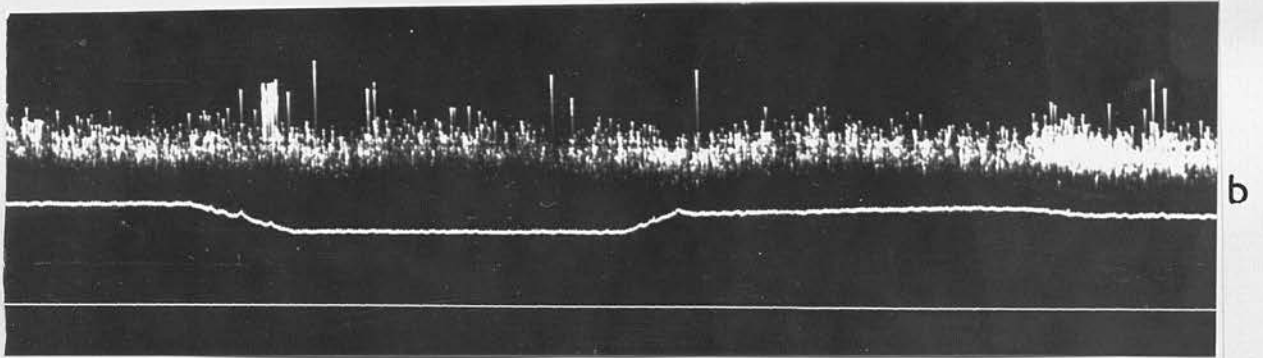
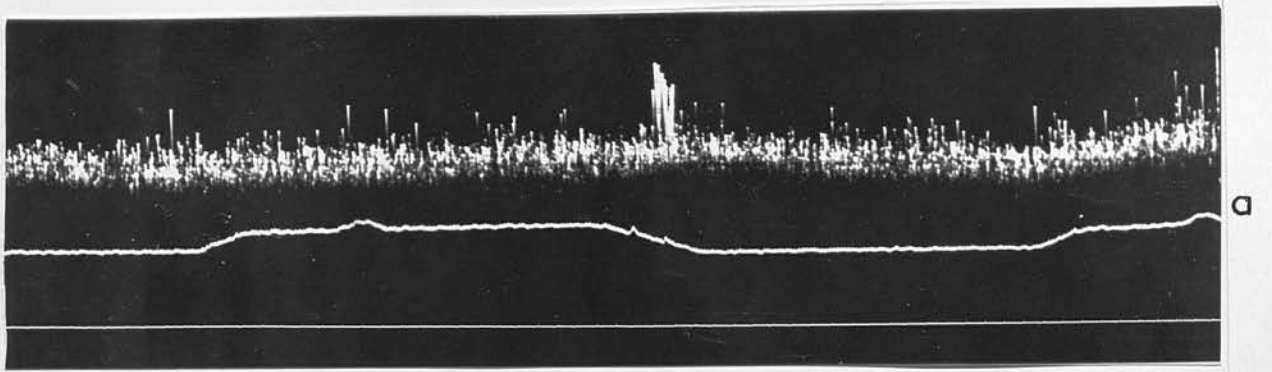
Directional unit. Conditions as above but bar is 5° long.

Directional unit. Conditions as above but bar is 25° long.

Directional unit. Black card passes over photocell on each side of receptive field in turn giving rise to two steps in the trace . The initial movement is in the null direction and there is no firing but upon return of the edge there is vigorous firing .

Directional unit . The arrangement is similar but the edge is passing in a direction at right angles to the null-preferred axis and firing occurs in both directions.

Directional unit. Firing in response to the movement of a 1° spot of light through the field in the preferred direction indicated by down of the monitor trace .Velocity $150^{\circ}/\text{sec}$.



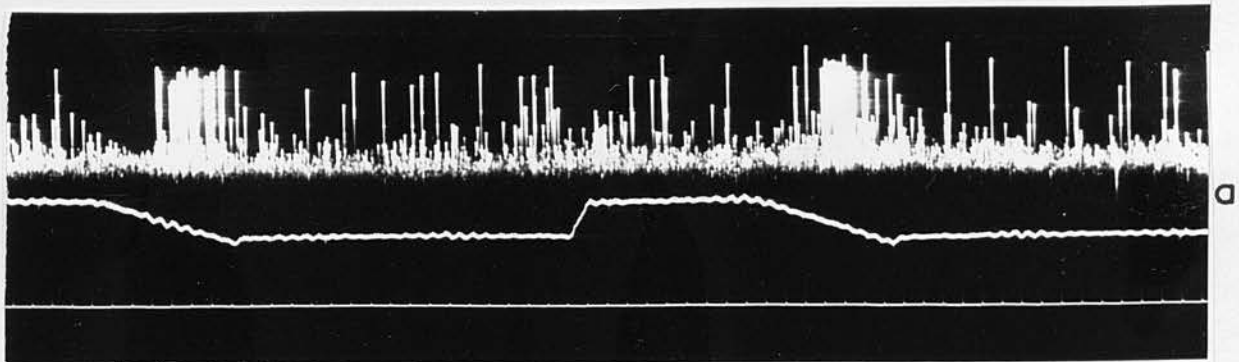
Directional unit as above but velocity $70^{\circ}/\text{sec.}$

Directional unit . As above but velocity $35^{\circ}/\text{sec.}$

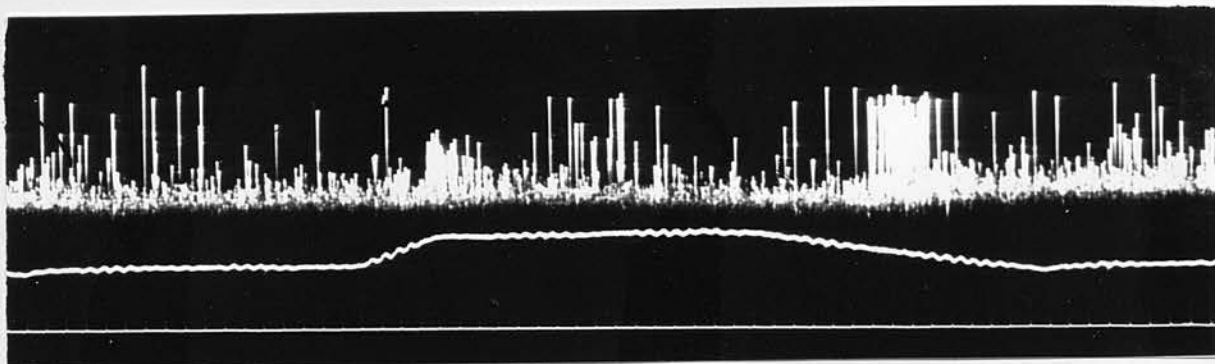
Directional unit. as above but velocity $6^{\circ}/\text{sec.}$

Directional unit. As above but velocity $0.5^{\circ}/\text{sec.}$

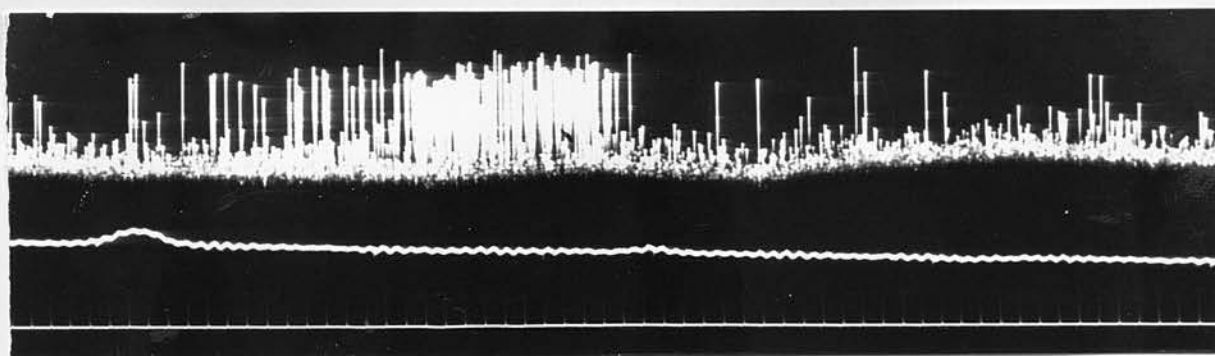
Directional unit. Firing in response to the movement of a 1° light spot in the null direction through the receptive field at $0.5^{\circ}/\text{sec.}$



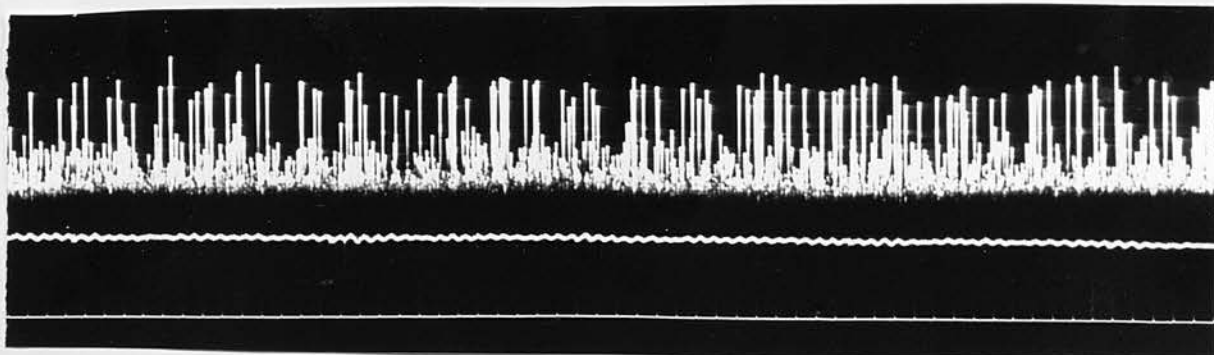
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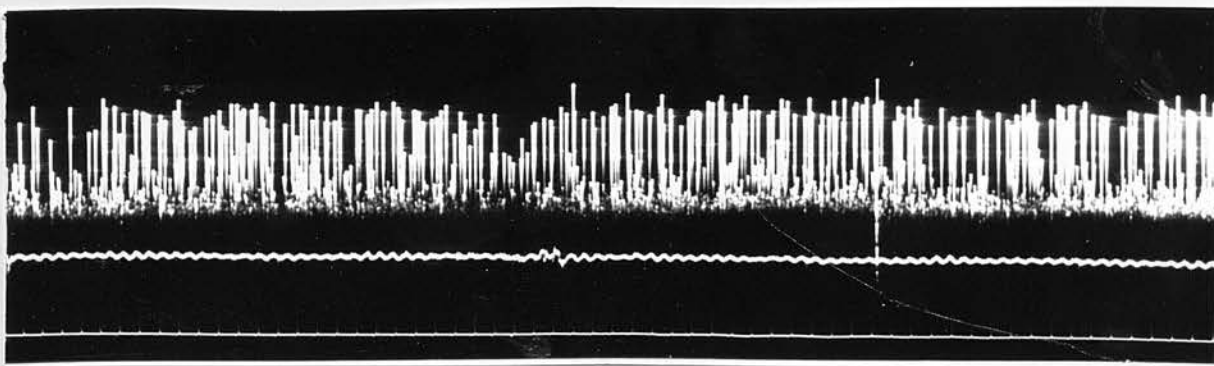
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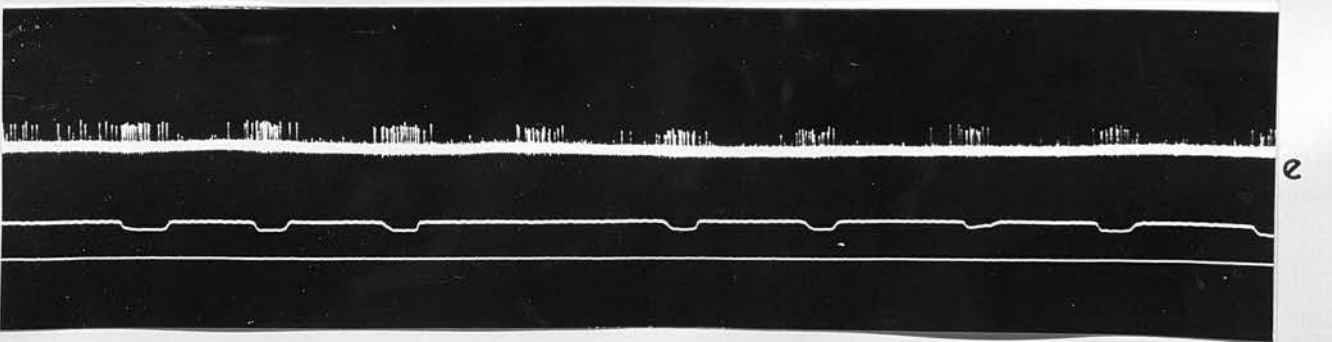
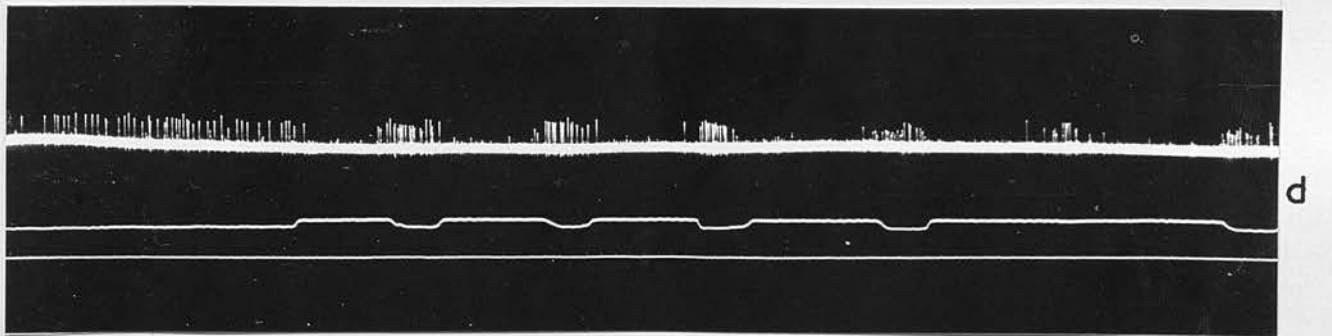
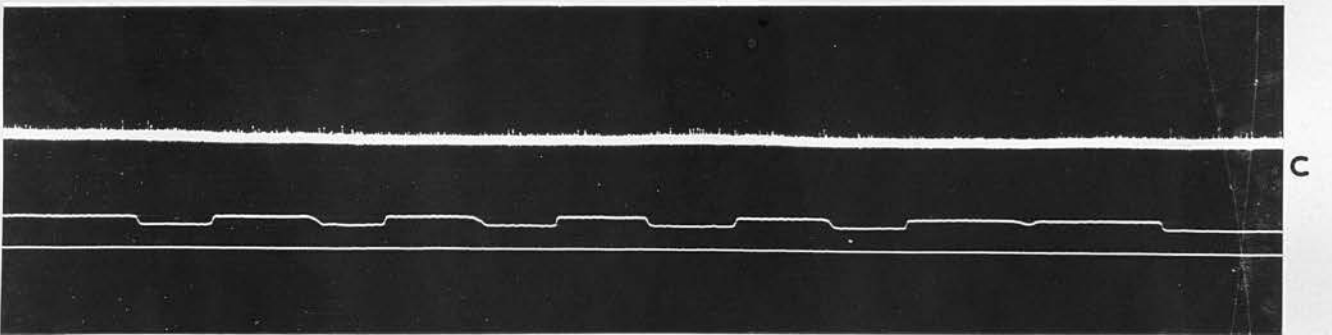
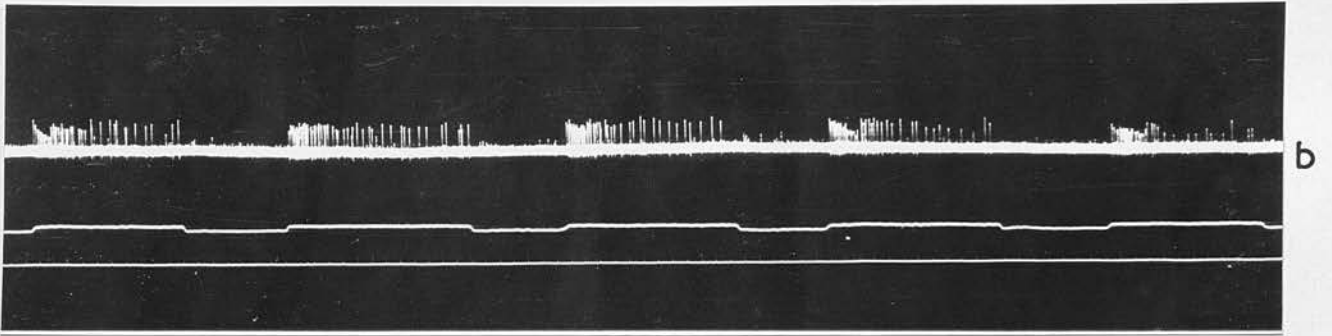
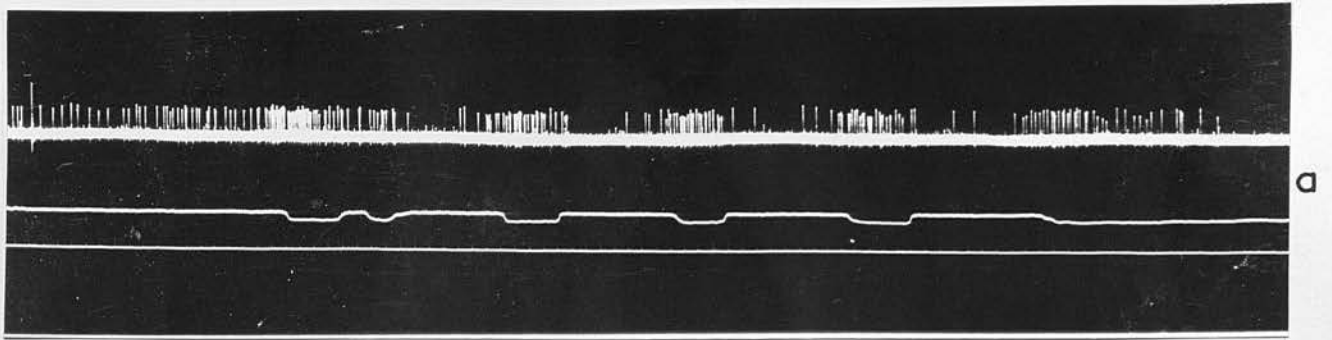
Adjacent on-off unit. Down of trace shows movement of a 3° white disc , against a black background, into on region of receptive field and causing firing .

Adjacent on-off unit. Down of trac shows movement of the disc into the off area but firing only occurs upon its removal .

Adjacent on-off unit. A 3° white disc was placed in the off field. A similar disc was moved in and out of the on field but inhibition from the off field is maintained and no firing occurs .

Adjacent on-off unit. Removal of the white disc from the off field causes an initial burst of firing and then firing of on field to entry of 3° white disc , down of trace , is again revealed .

Adjacent on off unit. The response of the on field is potentiated by 2 min of inhibition from the on field but the effect wears off with repetition.



DISCUSSION

Comparison of results with literature on the rabbit retina. The work of Thompson (1953) is the only published material dealing with the optic nerve units of the rabbit. The receptive fields which he describes are 10° or more in diameter, larger than almost all discovered in the present work, but his stimuli may have been rather diffuse because he used a system which projected light spots into the pupil plane. Two main classes of unit were described; (a) those showing an on and off discharge with an increased rate of firing in the intermediate on period and (b) units which gave an on-off discharge but do not have maintained firing during the on period. Thompson's death followed shortly after the publication of the paper and no more details were published.

It is of interest, however, to compare the optic nerve units with those found in the retina. Early studies of the retinal units (Granit, 1947) demonstrated the presence of three classes of unit; on, off and on-off, but no attempt was made at a detailed analysis of the receptive fields. A recent series of papers (Barlow, Hill & Levick, 1964; Barlow & Levick, 1965; Levick, 1965 and Levick, 1967) have demonstrated the great variety of units that may be recorded from the retina if suitably sophisticated stimuli are used. Barlow et al. (1964) sampled more units from the peripheral regions of the retina than from the visual streak. Levick (1967) has concentrated upon the units of the streak. It is clear, after examination of the percentage of the classes and the variety recorded, that the optic nerve sample described above is more akin to the units recorded from the periphery than to those of the visual streak. It is difficult to explain why this should be so for the ganglion cell count indicates that the optic nerve fibres of the streak should be by far the greatest in number and thus the most frequently encountered. Perhaps only the largest fibres were recorded and the sophisticated units of the streak are not represented in the population or it may be that the experimental techniques were not adequate to detect the units (stimuli not fine enough).

Barlow /

Barlow et al. (1964) describe a class of on and off centre concentric units in the rabbit retina for which a surround could be demonstrated but not mapped by a light spot flashed on and off. The nature of the response is not described but the illustrations show the transient response characteristic of the class 1 units above. The concentric units of Barlow et al. have a diameter of 3.2° on average compared with 2.4° for the class 1 population but his figures include those parts of the surround which were detected. A comparison of published proportions of these units in the total population gives,

	Barlow et al. (1964)	Levick (1967)	Hughes
on	25%	16%	15.6%
off	<u>23%</u>	<u>21%</u>	<u>25 %</u>
total	48%	37%	40.6%

The class 4, large field shadow sensitive units, are clearly identical to Barlow's large field off units. He does not describe the on type which forms a small proportion of the class in the present study. These off units are described by Barlow et al. as being most effectively stimulated by fast movement within the field but records have been obtained indicating a pronounced response over the range of 0.3° - 160° per second. There is a considerable difference between the number of these units recorded in the peripheral retina (Barlow), streak retina (Levick) and the optic nerve.

	Barlow et al.	Levick	Hughes
on	-	-	4.4%
off	<u>11%</u>	<u>4.7%</u>	<u>17.8%</u>
total	11%	4.7%	22.2%

The class 4 units have the largest fields of the commonly recorded unit types. It is likely that they correspond to the large ganglion cell population which appears to possess extremely extensive dendritic trees. The /

The ganglion cell diameter distribution shows a change from 10% to 23% in the proportion of the total distribution represented by cells more than $15\ \mu$ in diameter when moving from streak to the periphery. It is suggested that this is the basis for the difference between the figures of Levick and Barlow et al. The higher proportion of the units found in the optic nerve would presumably result from the larger diameter of the axons of this class of ganglion cells. Many low amplitude units have to be discarded in recording from the optic nerve and these may represent the peak of the fibre diameter distribution. The result could be that the class from, say $3-6\ \mu$ in diameter is over-represented. In recording from the retina the smallest ganglion cell recorded will be about as big as the largest axon in the optic nerve so that a more representative sample may be obtained.

There is no difficulty in establishing the identity of the directional units recorded by the different workers. The sample recorded from the optic nerve were all about 3° in diameter and were of the on-off type. No field directional units were recorded.

	Barlow	Levick	Hughes
on	11%	7%	-
on-off	30%	10%	9.1%
	<hr/>	<hr/>	<hr/>
total	41%	17%	9.1%

The on and off adjacent units described above are similar to those termed orientation detectors in the papers by Levick (1965 & 1967). The units ^{account} for 1.7% of the total sample in the optic nerve and 11% in the streak region of the retina. It should be noted that although the units respond selectively to the orientation of a projected slit flashed on to the receptive field they differentiate between movement along two perpendicular axes. Movement across both fields produces no response in either direction while movement across each field in turn elicits a response in both directions. The units might be termed axial movement, rather than orientation, detectors. Until evidence of their natural function is obtained it is perhaps better to avoid/

avoid the function orientated terminology and use the descriptive.

Barlow's work was carried out in the dark adapted animal and the field changes of the dark adapting unit (class 2) would not have been noticed. Under conditions offering a wider range of intensities than those used in this work it might be found that this class simply represents the extreme case of properties associated with the remainder of the concentric units. Units responding most rapidly at the highest light intensities would obviously be more likely to be noticed. A similarly rapid alteration in the receptive field organisation of monkey LGN cells has been described by Wiesel and Hubel (1966) as occurring during dark adaptation. The change occurred within about one second as did the re-organisation of the field described above.

The presence of maintained activity in records from some cells was noted by Barlow et al. (1964) but was not used in the classification because of the possible dependence of the activity on the anaesthetic level. The reasons for including maintained activity in the classification of the optic nerve units have already been given and, in any case, all of the factors examined are potentially subject to the influence of anaesthetics. The paper by Barlow, Hill and Levick appears to reflect a certain degree of confusion about the response characteristics of the different unit classes. On page 400 it is stated that

"Certainly the rapid movement type adapts more rapidly than the concentric type, but amongst the latter there is also considerable variation."

On page 391, however, it is stated that

"In many units of the first series with large fields and the ability to respond to fast movements, the action potentials were unusually large and well isolated, and they often had a vigorous maintained discharge that increased or decreased when the general level of illumination was changed."

The reference in the first quotation to the rapid adaptation of the "rapid movement type" (large field off units) clearly conflicts with the claim of a maintained /

maintained response in the second. The illustration of page 394 (Barlow, 1964) shows the response of an on and of an off concentric unit. Both types, as my own results would suggest, show responses of the rapidly adapting type and could hardly be exceeded in adaptation rate by the large field off units as is claimed on page 400. The separation of the maintained units in a class of their own is felt to be justified for the present and may be supported by a more sophisticated investigation of their properties. The manner in which Barlow et al. (1964) classified this group is not clear. In the optic nerve the on type form 12.6% and the off type 13% of the total.

No units recorded from the optic nerve revealed the properties of local edge detectors (19.5%, Levick, 1967), or uniformity detectors (4%, Levick, 1967). On the other hand, neither Barlow et al. nor Levick mention the giant field units which form 0.9% of the optic nerve sample. The localisation of the units in the visual field of the animal was noted in the earlier experiments but the arrangement of the apparatus in the later did not facilitate the observations and they were discontinued. The units sampled tend to lie in the nasal field and show a fairly uniform distribution. The need to avoid the medial blood vessels of the optic nerve necessitates the insertion of the electrode in the lateral regions where the fibres representing the nasal field are represented. Searches for differentiation of unit function across the retina are best carried out when recording from the retinal ganglion cells so that localised populations may be sampled at will and their position noted.

THE MECHANISM OF THE DIRECTIONAL UNIT

INTRODUCTION

Barlow and Levick (1965) have subjected the directional unit to an intensive analysis which culminates in the constitution of a model for its behaviour. The general acclaim which received the model is deserved but tends to ignore its provisional nature. The account below includes a summary of the argument of Barlow and Levick followed by a critical examination of their assumptions.

Observations of Barlow and Levick.

1. Directional units respond to both on and off of a light spot flashed at all points within the receptive field.
2. A directional response is obtained to the movement of stimuli darker or lighter than the background.
3. If movement is exceedingly slow in the null direction then firing occurs.
4. The directional property of the field is present in all regions except for a small peripheral area about $\frac{1}{2}$ -1° wide.
5. The smallest displacement over which a directional response may be elicited ranges from 0.1°-0.4°.
6. A spot moved in the null direction above the threshold velocity produces no firing whatsoever.
7. A spot moved in the null direction which is halted within the receptive field and then moved once again elicits a response as the movement is initiated.

Reasoning of Barlow and Levick.

- (1) The on and off systems are assumed to be able to be treated independently of one another on the basis of evidence, mentioned but not disclosed, to the effect that their summation occurs below the level at which the property of directionality is organised.
- (2) The directional response could result from the propagation of either facilitation in the preferred direction or of inhibition in the null direction. The former possibility is unlikely for firing would not occur in the null direction after a stationary spot is moved, 7., if the directionality were /

were obtained by facilitation. The phenomena are in accord with the propagation of a wave of transient inhibition in front of the moving spot. Firing in the null direction, 3., supports this concept and indicates that below the threshold velocity the inhibition dies away before the spot reaches the inhibited area.

(3) The complete absence of firing in response to movements above the threshold velocity in the null direction shows that the inhibition must be projected ahead from one level in the system to a lower one at some distance ahead. If this were not the case then the abolition of the response at an adjacent point in the null direction would also inhibit the spread of inhibition from this point to the next.

(4) The displacement threshold for a directional response indicates

"that the complete mechanism for directional selectivity is contained within a subunit of the receptive field extending not much more than $\frac{1}{4}^\circ$ in the preferred - null axis. Since the result does not depend critically upon the position of the slit within the receptive field, it looks ..., as if the sequence discriminating mechanism must be reduplicated perhaps a dozen or more times to cover the whole receptive field."

(5) "Sequence discrimination is assigned to bipolar cells because the ganglion cell appears to pick up from subunits that are replicated in different parts of the receptive field, and bipolar cells are the replicated anatomical elements that feed ganglion cells."

(6) The inhibition is agreed to not act from receptor to receptor for the distances involved appear too short.

"Presumably then it runs from receptors to bipolar cells."

"Since the horizontal cells are known to have processes conducting laterally the natural starting hypothesis is that they are the cells carrying this inhibition from one region to another."

Comment. The chain of reasoning in the above paragraphs clearly begins to weaken at stage (4) above where the correlation of anatomy and physiology starts /

starts. A few extra clues about the inhibitory mechanism can be obtained by careful examination of the results shown in table 3 of Barlow and Levick (1965). These have been displayed below in graphical form to suit our purposes (fig. 53). Two 0.1° slits were illuminated from behind, first individually and then in a sequence AB and BA at constant temporal but varying spatial intervals. The number of spikes occurring at on and at off of the lights were counted and tabulated. The graph shows the number of spikes occurring at either on or off for a sequence in the null, BA, direction and the preferred, AB, direction as well as the total number of spikes for A and B flashed alone.

A comparison of firing at both on and off in the null and the preferred direction shows that in response to these stationary stimuli the null inhibition spreads for at least 0.75° . The inhibition is extremely marked at a slit separation of $8'$ and has been noted to be vigorous at $6'$. As the slit is of finite width it must be noted that the minimum distance actually tested is more in the order of $10'$. The extrapolation of the graph to smaller separations is not justified and the necessary data is not available. The appearance suggests that inhibition would not cease immediately and might be present at a separation of about $5'$. Until this information is obtained we are justified only in the assumption of about $10'$ minimum for the directional effect.

What does the $10'$ minimum and the 0.75° maximum for inhibitory spread indicate about the nature of the inhibitory connections?

- (a) the minimum may be the distance within which movement can occur without transgressing the limits of the unit upon which inhibition acts.
- (b) it is possible that the $10'$ interval represents the distance between the points of reception and generation of inhibition.
- (c) the 0.75° limit to the inhibitory effect comes about as a result of either inhibitory processes which extend that distance or of synaptic interconnections between the inhibitory units.

In terms of distances along the retina the lower limit to the directional effect /

effect is about 30μ and the upper 125μ . It is possible to derive an estimate of the time course of the inhibitory process from these dimensions. The null response to high velocity movement ($150^\circ/\text{sec.}$) establishes the rapid initiation of the inhibition. The $0.5^\circ/\text{sec.}$ velocity threshold for null direction firing is $85\mu/\text{sec.}$ on the retina so that such a stimulus traverses about 3 minimum distances per second. The inhibition thus lasts for no more than $\frac{1}{3}$ second or less if the threshold displacement is found to be smaller.

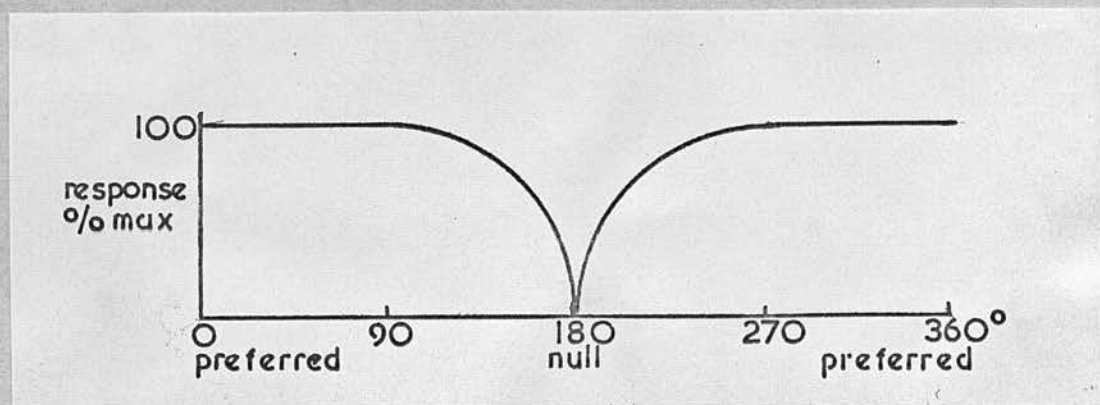
Examination of the evidence available in Barlow and Levick's paper shows nothing which positively supports the attribution of the inhibitory process to the outer plexiform layer or, more specifically, to the horizontal cells. Barlow and Levick are simply concerned with the explanation of one type of inhibition but it seems likely that this will have mechanisms similar to those involved in the centre-surround interplay, edge detection, orientation detection, etc. These processes are usually assigned to interaction between elements at the inner plexiform layer.

Dowling, Brown and Major (1966) investigated the organisation of the rabbit horizontal cells. Brown and Levick use the type which possess a clump of processes at some distance from the main body of the cell in their diagram. This form of cell is rare and the gap between the major and minor clump is in the order of 100μ which is rather large for the threshold displacement of the directional response if main cell body is regarded as the receptive area and the distal clump as the region for initiation of inhibition. As Barlow and Levick assumed, the horizontal cells show connections to the receptors and to bipolar dendrites and soma. These connections do not, however, display the spatial separation necessary to their theory. Single processes show connections to both bipolar and receptor and possess the characteristics of axon and dendrite.

In view of the above findings are there any attractive alternative models? It appears very improbable, on the grounds of parsimony alone, that the inhibition occurs at the receptor level. Inter^eceptor connections are /

are too short to account for the present minimal displacement. If, however, the directional threshold displacement is found to be much smaller than such an explanation might have to be envisaged for the 30μ value is about the same size as a bipolar 'tight' dendritic tree. At present it appears that the inhibition occurs between these bipolar units as Barlow and Levick suggest. Simple laterally inhibiting interconnections between the bipolars are not an adequate explanation of the 125μ spread of inhibition in the null direction. In spite of the reluctance of Barlow and Levick to postulate esoteric properties for the inhibitory unit it appears that this is to some extent necessary. The data suggest a unit conducting in one direction only for up to 125μ in which the passage of activity can be initiated from any point along the path. One possibility is that small interconnected amacrine cells are activated by the bipolars and block transmission to the ganglion cell but more experimental data is required before such allocations of function can be made.

Response in the preferred direction. If the inhibitory processes spread across the directional unit receptive field in the null direction alone, as is suggested by Barlow and Levick, then it might be expected that objects moving into the field at right angles to the null direction axis would not generate any component of inhibition. Firing would be found to increase when moving in along successive radii of the field from the null direction to that perpendicular to it and would then remain constant until the preferred direction was reached. The response would be like this -



In fact one illustration of Barlow, Hill and Levick (1963) shows that firing increases as approaches are made along successive radii from the null direction all the way round to the preferred direction but no comment is made on this feature. The flashing slit experiment (fig. 53) also shows a degree of facilitation of firing in the preferred direction but again no explanation was offered.

METHODS

In order to ascertain whether the increase of firing from the null to preferred direction was a common property of the directional units: five units (1 LGN cell and 4 optic nerve) were studied quantitatively. A projected bar was moved against a dark background with its long axis at right angles to the direction of movement along various radii of the receptive field. The number of spikes occurring in the total response to leading and trailing edges was added and plotted as a percentage of the maximum response against the angular orientation with respect to the preferred direction.

RESULTS

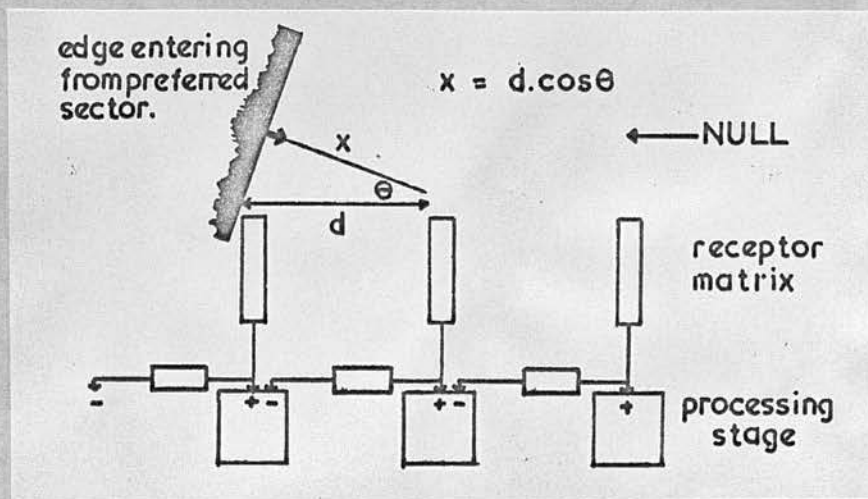
A typical set of responses for radii subtending 45.0° to each other is shown in fig. 54 while fig. 55 displays the responses of the various units. In all cases the apparent facilitation in the preferred direction was marked.

DISCUSSION

A number of complex reasons for facilitation in the preferred direction may be postulated but the most likely explanation is that it results in some way from the stimulation of the inhibitory system in the reverse direction. The variation in the effect as the angle of the radius of stimulus entry relative to the null - preferred axis is altered appears to be roughly proportional to the vector component of the motion along the preferred axis. The suggested explanation is as follows.

Imagine /

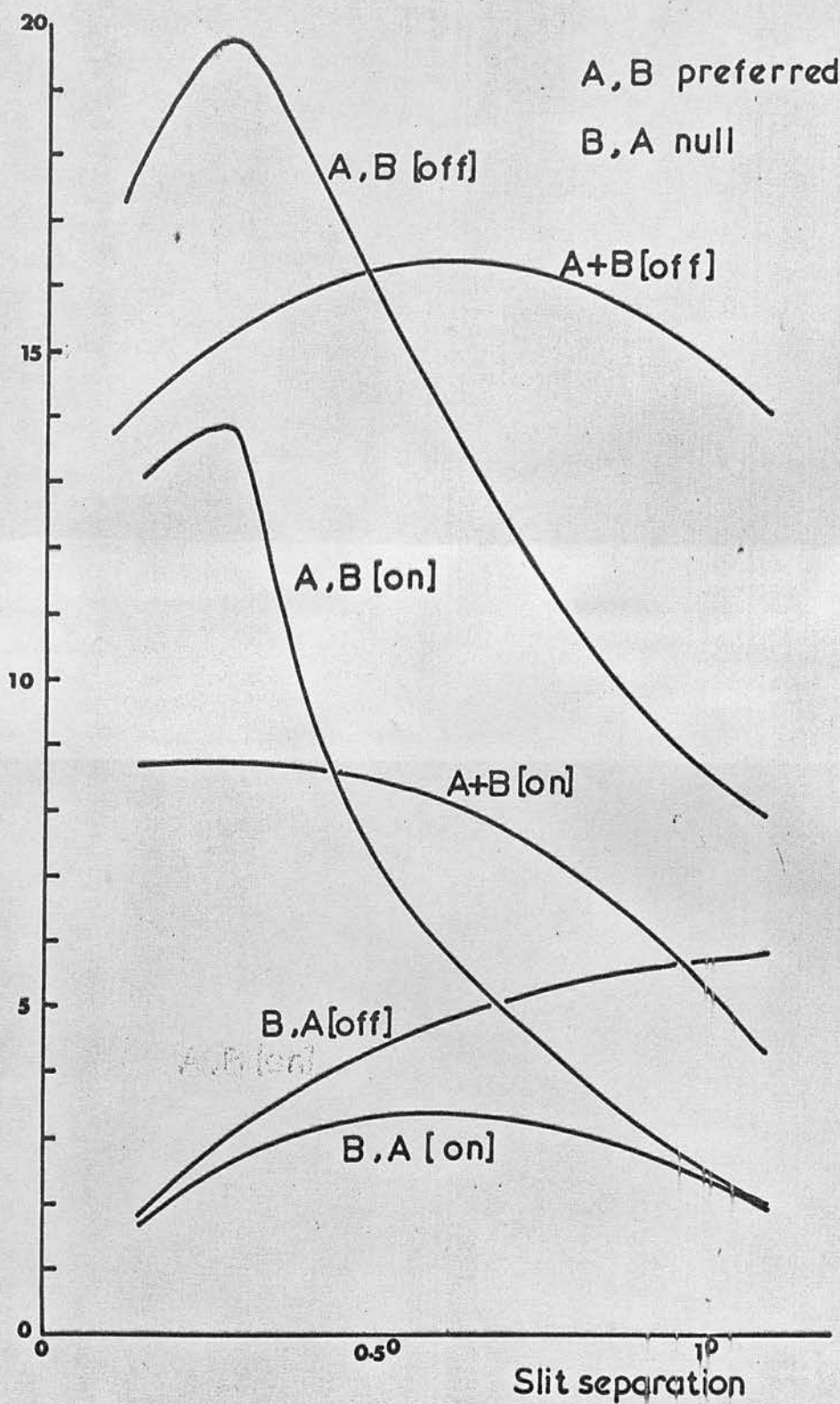
Imagine an edge, orientated parallel to the null direction, moving across the field at right angles to the null - preferred axis. At the moment of stimulation of a region of the receptive field a response will be elicited which will be almost immediately out short by inhibition passing in the null direction from a simultaneously stimulated nearby point. Entry to the field from a radius of the null sector ensures greater inhibition because the inhibition from a stimulated point arrives somewhat ahead of the edge. Entry of the edge along a radius in the preferred direction will bring about stimulation of a region followed at some time later by inhibition from a point ahead subsequently stimulated by the moving edge. The minimum inhibitory spread (displacement threshold for a directional response) is labelled and represented by a short interneurone. The distance moved by the edge, x , in traversing the distance d decreases as the entry angle θ increases. At constant velocity the interval between stimulating subunits will vary as $d \cdot \cos \theta$. As conduction takes finite time and the inhibition must also require time for initiation it would appear likely that the edge will reach a region of peak inhibition only at entry angles within the inhibitory sector so that total inhibition of the response would occur over a sector of less than 180° , as is found to be the case.



The above model gives an adequate explanation of the increase in firing in the preferred direction in response to moving stimuli but does not explain the effect of slit separation on the sign of the interaction between stationary stimuli activated in sequence in the preferred direction. This latter effect is also apparent in results of Barlow and Levick but is not mentioned in their discussion.

The quantitative results so far obtained appear to be in quite good agreement with predictions of the above model. In fig. ⁵⁵ the pooled results from four directional units displayed in one semi-circle of the polar plot. On the other, right hand, side of the plot is shown the firing pattern predicted for one of the units on the left if the model were valid. The prediction may, of course, be made only for the preferred sector. The correspondence between the theoretical and experimental curves may readily be seen. More accurate tests must, however, be made before the explanation may be fully accepted.

Fig. 53 Slit separation in degrees is plotted against the number of spikes obtained in response to the presentation of two slit stimuli in various spatial combinations. See page 66 for explanation.



After results of Barlow & Levick (1965)

Fig. 54 The response of an optic nerve directional unit to the movement of a 2° wide by $\frac{1}{2}^\circ$ white bar into the field along successive radii of entry separated by 45° . The bar was orientated perpendicular to and symmetrical about its axis of motion. The responses to movement in the null and preferred directions are indicated by N and P respectively. The unit was spontaneously active and this activity may be seen to be inhibited by movement over the ninety degrees of the null sector tested.

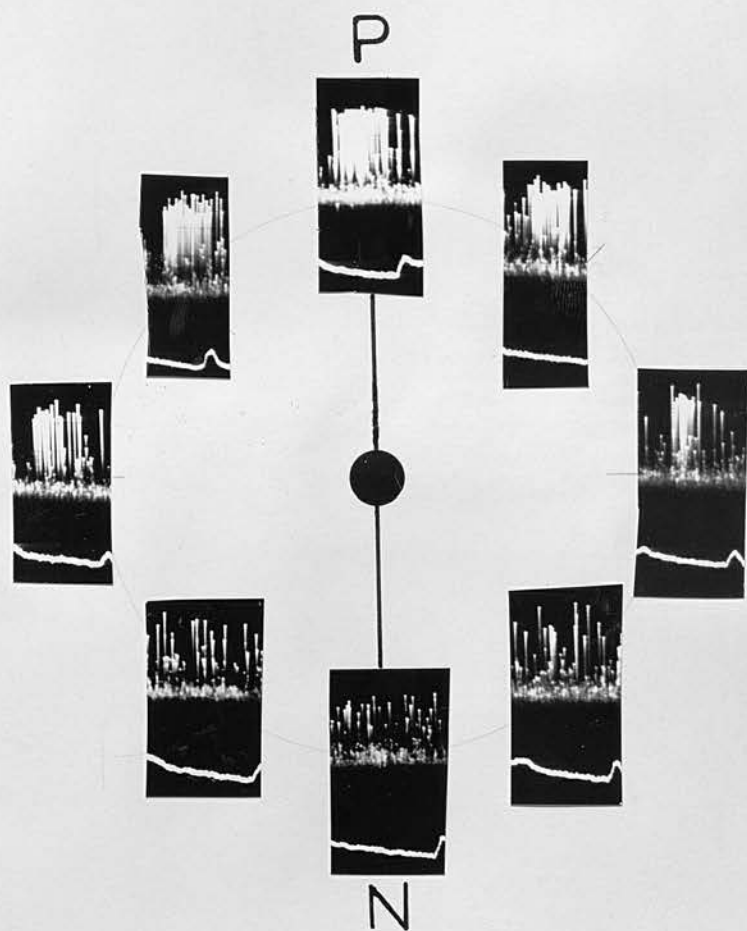
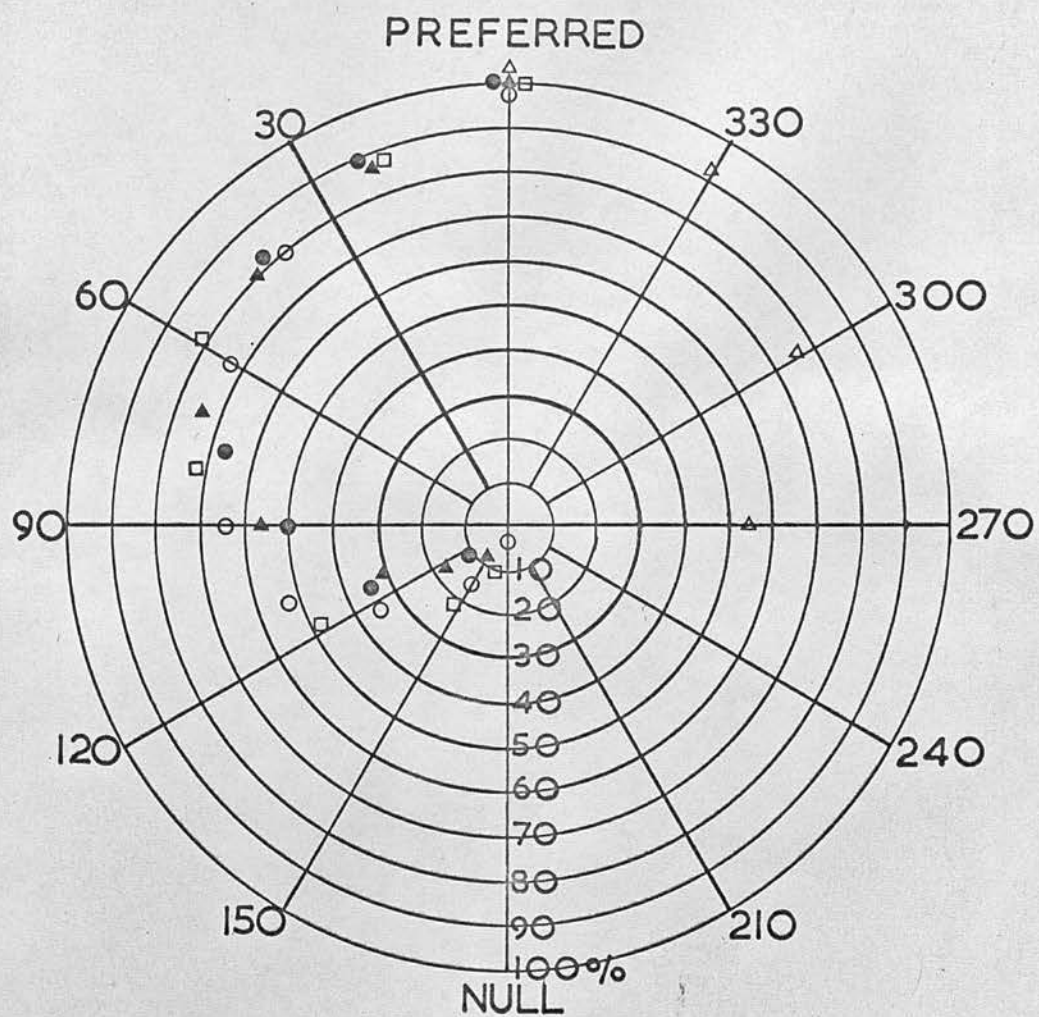


Fig. 55 A polar plot of firing of a directional unit for different radii of stimulus entry into its receptive field expressed as a percentage of the maximum response to entry in the preferred direction. The results are from four units indicated by various symbols in the left half of the plot. The significance of the right half of the plot, white triangles, is described in the text on page 71.



PRIMARY TERMINATIONS OF THE OPTIC NERVE

The recent literature contains no account of the central connections of the rabbit optic nerve. Le Gros Clark's review of the mammalian visual pathways (1942) is somewhat out-of-date and the more recent article by Meikle and Sprague (1964) deals only with the cat. References mentioned below deal with the rabbit unless some other animal is named.

OPTIC CHIASM

The optic nerves of the rabbit meet shortly after entering the cranial cavity through their respective adjacent foramina and travel together for a short distance before they join together to form the chiasm. In sections of the chiasm, bundles of fibres may be seen to interweave as they decussate. An early description of the optic tract after it leaves the chiasm suggests that no uncrossed fibres are present (von Gudden, 1870). Subsequent workers are agreed, however, that uncrossed fibres are present but form only about 10-15% of the tract (Pavlov, 1900; Loepp, 1911). The uncrossed fibres are described as being spread diffusely throughout the optic tract. The work of Brouwer (1923) confirms this view rather than denies it, as is stated by Choudhury (1964), and adds that the fibres are more numerous in the dorsal half. Brouwer describes the fibres as crossing from medial to lateral, superior to inferior and vice versa respectively in the chiasm. Many fibres may be seen to branch at the chiasm in the rabbit (Cajal, 1911) but the fraction of uncrossed fibres arising in this fashion is not known. Lesions of the inferior retina bring about dorso-lateral optic tract degeneration while those to superior retina cause the degeneration in the medio-ventral region.

LATERAL GENICULATE NUCLEUS PARS DORSALIS

All authors are agreed that the removal of one eye is followed by a massive degeneration in the contralateral dorsal LGN. The incoming fibres of the optic tract spread around the lateral and ventral boundaries of the nucleus. Within the nucleus the fibres form a complex interdigitating network /

network in whose meshes lie the cells upon which the fibres terminate. The medial wall of the geniculate is free of degenerating optic fibres (Brouwer, 1923; Loepp, 1911; Cragg, 1962).

On the ipsilateral side, the number of degenerating fibres is considerably smaller and, according to Brouwer (1923), they are confined to the most medial edge of the nucleus. Cragg (1962) describes a narrow vertical strip of degenerating fibres terminating at the medial margin of the nucleus and covering a region about 100 μ wide. This region is confined to the most posterior three fifths of the dorsal nucleus.

The presence of this medial region of bilateral innervation in the rabbit is clear in the results of Brouwer (1923), Overbosch (1927) and Minkowski (1920). A similar area is described in the rat by Lashley (1934). Hayhow, Sefton and Webb (1962) have found that three minima appear in the density of the crossed fibre terminal degeneration in the rat. These regions coincide with maxima in the uncrossed terminal density on the contralateral LGN. The arrangement thus gives the appearance of laminations. Packer (1941) has produced evidence that the crossed and uncrossed fibres end in different laminae in the phalanger (marsupial) LGN. Similar potential lamination has been reported in the case of the ferret (Jefferson, 1940). Brouwer (1923) comments that the region of crossed fibres in the rabbit LGN evinces an area of reduced degeneration which corresponds with the site of uncrossed fibre termination (p. 120). In view of the more developed form of the rabbit visual system it appears likely that the features discovered in the rat will be found to be present upon reinvestigation.

LATERAL GENICULATE NUCLEUS PARS VENTRALIS

The confused literature concerning this region reflects the inadequacies of the common means of tracing out fibre connections. Cragg (1962, Nauta), Loepp (1911, Marchi), Brouwer (1923, Marchi) and Pavlov (1900, Marchi) all agree that fibres of the optic tract pass into the ventral nucleus of the LGN. The majority of these fibres clearly pass through the nucleus to the dorsal /

dorsal nucleus and terminate there (Loepp, 1911; Brouwer, 1923). Since Cajal (1911) used the Golgi method to demonstrate the termination of collaterals of these fibres in the ventral nucleus of the LGN of a number of mammals including the rabbit, it has been generally accepted that the ventral nucleus is a site of primary terminations. Such evidence does not, however, establish that the retinal fibres terminate in the nucleus. Pavlov (1900) and Brouwer (1923) both observed a limited number of terminations of degenerating optic nerve fibres in the rabbit ventral nucleus. All of the above authors and Minkowski (1920) have described only contralateral degeneration. Hayhow et al. (1962) found a massive contralateral and lesser ipsilateral projection to the pars ventralis of the rat LGN.

SUPERIOR COLLICULUS

The majority of the optic fibres which pass across the dorsal surface of the LGN and continue, in the brachium of the superior colliculus, over the roof of the midbrain in the thalamic stratum zonale terminate in the superior colliculus. The crossed projection to the colliculus is generally accepted to be quite massive but no count of the fibres has been made (Pavlov, 1900; Loepp, 1911; Brouwer, 1923). Pavlov (1900), Brouwer (1923) and Overbosch (1927) claim that there is no ipsilateral collicular projection in the rabbit. Loepp (1911), Minkowski (1920) and Cragg (1962) describe a noticeable but less considerable uncrossed projection in the same animal. Uncrossed projections have been observed in the cat (Altman, 1962; Singleton & Peele, 1966), rat (Hayhow et al., 1962) and opossum (Bodian, 1937).

The optic fibres of the crossed representation are usually described as terminating most densely in the upper portion of the stratum opticum and in the stratum griseum superficiale (Pavlov, 1900; Loepp, 1911; Brouwer, 1923) in the rabbit, (Altman, 1962; Singleton & Peele, 1966) in the cat and (Hayhow et al., 1962) in the rat. Lund (1966) found the crossed fibres to terminate evenly throughout the stratum opticum and to pass up into the stratum griseum superficiale as far as the stratum zonale in the rat.

Brouwer /

Brouwer (1923) and Loepp (1911) found the stratum zonale of the rabbit to be free of Marchi degeneration but Ganser (1882), Tartuferi (1884) and Minkowski (1920) describe such a projection. The latter results are in agreement with those of Hayhow et al. (1962) on the rat, Bodian (1935) on the opossum and Jefferson's work on terminal degeneration in the colliculus (1940). Although Cajal (1911) claims that no fibres of retinal origin turn down to the deeper layers of the colliculus, they have been reported in both rat (Lund, 1966) and cat (Altman, 1962).

The ipsilateral fibres terminate in a more circumscribed region of the colliculus. Loepp (1911) describes their endings as confined to the stratum opticum. Similar results have been reported for the rat (Hayhow et al., 1962) and opossum (Bodian, 1937).

ACCESSORY OPTIC SYSTEM

The accessory optic tracts branch off from the main optic tract during its course back from the chiasm to the lateral geniculate nucleus superior colliculus.

Anterior Accessory Optic Tract. The anterior accessory optic tract of Bochenk (1908) has been described in the rabbit as branching off from the optic tract caudal to the chiasm and running along the diencephalon to terminate in the subthalamic nucleus of Luys (Loepp, 1911; Pavlov, 1900). Overbosch (1927) claimed that the tract consisted of aberrant optic tract fibres. By means of silver, rather than Marchi, staining methods for the fine fibres, Biolli has shown (1961) that the fibres carry on more caudal than the nucleus of Luys and terminate in the nucleus of the transpeduncular tract. The anterior accessory tract is composed only of crossed fibres. This description corresponds with that of Hayhow, Webb and Jervie (1960) for the rat. These workers proposed the more appropriate name of the inferior fasciculus of the accessory optic system for the tract. This fasciculus is apparently not present in the cat (Barris et al., 1935).

Posterior Accessory Optic Tract and Tractus Peduncularis Transversus.

The /

The posterior pair of accessory optic tracts was described by Gudden (1870) and termed the tractus peduncularis transversus. Some subsequent workers have called it the posterior accessory optic tract. Giolli (1961) describes the transpeduncular tract as diverging from the superior quadrigeminal brachium and passing around the superficial midbrain to enter the tegmentum medial to the cerebral peduncle. The tract terminated in the nucleus of the transpeduncular tract (medial terminal nucleus of the accessory optic tract). In the rabbit the transpeduncular tract contains 2,800 to 3,700 fibres of which $\frac{1}{2}$ to $\frac{2}{3}$ originate in the retina. The tract lies adjacent to the anterolateral edge of the superior colliculus.

Le Gros Clark (1931) describes a small bundle of accessory optic fibres as arising from the optic tract prior to the medial geniculate plane and as passing down across that nucleus to terminate in the nucleus of the transpeduncular tract. In the generalised mammalian brain described, this tract is regarded as identical to the tractus peduncularis transversus of earlier workers. As Giolli indicated (1961), the transpeduncular tract of the rabbit arises from the brachium of the superior colliculus and not from the optic tract. The fibres described by Le Gros Clark (1931) form a separate group which was described by Bochenk (1908) as the posterior accessory optic tract.

Munzer and Wiener (1902) observed the posterior fibres of the tractus peduncularis transversus to come into connection with a small nucleus situated at the rostrolateral edge of the superior colliculus. This nucleus was called the n. suprageniculatus and apparently corresponds with the n. parageniculatus of Loepp (1911) which was described as a primary termination for optic fibres. This nucleus has been observed in the rat by Hayhow et al. and was termed the dorsal nucleus of the accessory optic tract (1960). A lateral nucleus on the ventral margin of the medial geniculate nucleus was also described.

The relations of the dorsal nucleus of the accessory optic tract and the nomenclature of the system have been further confused by the papers of Marg /

Marg (1964) and Hamasaki and Marg (1962) on the electrophysiology of the optic tract. It is their claim that the anterior accessory optic tract and the direct transpeduncular fibres to the nucleus of the transpeduncular tract are non-functional in the rabbit. It is their argument that the nucleus of the transpeduncular tract is supplied by the dorsal nucleus of the accessory optic tract, which they choose to call the nucleus of the posterior accessory optic tract, and that a synapse thus intervenes before the fibres of the transpeduncular tract reach their terminal nucleus. The argument is based on rather doubtful electrophysiological evidence.

Hayhow et al. (1960) have contributed greatly to the rationalisation of nomenclature in the system of the accessory optic tract. The anterior accessory tract was found to terminate in the dorsal part of the nucleus of the transpeduncular nucleus of the rat and is called the inferior fascicle of the accessory optic system. The remaining fibres which branch off from the optic tract (posterior accessory tract of Bochenk) and from the brachium of the superior colliculus (t. transversus ped.) to terminate in the dorsal, lateral and medial terminal nuclei are referred to as the superior fascicle of the accessory optic tract. This nomenclature is sensible, applicable to the rabbit, and will be used subsequently.

In all animals studied, the superior fascicle of the accessory optic system has been described as entirely crossed by the majority of workers. Gillilan has demonstrated the superior fascicle as present in the cat and monkey (1941). No uncrossed fibres are present, even in the monkey (Giolli, 1963).

THE PRETECTUM

Hayhow et al. (1962) have pointed out that, since the work of Clark (1931) and Magoun and Ranson (1955), the pretectal area has been accepted as an anatomically discrete optic terminal centre which mediates the pupillary light reflex. The anatomical evidence for the presence of optic terminals in the region has remained, however, rather scant. In the rabbit, Loepp /

Loepp has described degeneration in the nucleus parageniculatus which lies adjacent to the anterior tectum (1911). Apart from this only Kuhlenbeck and Miller (1942) have mentioned the optic terminals in this region of the rabbit brain. Their observations were carried out on normal material and indicated that optic fibres enter the nucleus of the optic tract (*n. lenticularis mesencephali magnocellularis*) and its continuation, the *n. olivaris colliculi superioris*. It appeared probable that fibres entered both the area and nucleus praetectalis. In the rat, Hayhow (1962) has found terminals of the optic tract in both of these nuclei, which are the only ones included in Clark's pretectal region. Bucher and Nauta's (1954) medial nucleus of the optic tract, deep pretectal *n.* and medial pretectal area do not appear to receive optic terminal fibres. The description of terminals in the cat (Altman, 1962 & Singleton & Peele, 1966) is similar to that of the rabbit and rat. The projection is predominantly crossed in both rat and cat. A very few uncrossed fibres are present within the nuclei.

THE PULVINAR

The degenerating fibres seen in the pulvinar after unilateral enucleation are generally agreed to belong to bundles passing through the region to the pretectum and colliculus (Brouwer, 1923; Loepp, 1911) for the rabbit, (Hayhow et al., 1962) for the rat and (Altman, 1962) for the cat.

THE RETINO-HYPOTHALAMISCHE BAHN

A considerable body of evidence suggests a projection from the visual pathways to the hypothalamus but this is mainly derived from work on the light dependence of various visceral activities. The most important of the suggested retino-hypothalamic paths is that of Knoche (1957) and Blumcke (1958) which has been observed in rabbit, dog and man. The fibres are said to be non-myelinated and to proceed from the rostral chiasm to the hypothalamus, infundibulum and hypophysis. Hayhow has failed, however, to demonstrate the path in either rat (1960) or cat (1958). It is, at present, not clear whether the path exists or not.

SINGLE UNITS OF THE BRACHIUM

The fibres of the brachium of the superior colliculus form a layer about 0.3-0.5 mm. thick over the surface of the midbrain just anterior to the superior colliculus. The recording of single units from this group of fibres is of interest because it may reveal the nature of the input to the stratum opticum of the superior colliculus whose small fibres are difficult to isolate within that organ. No serious attempt to record from the brachium was made but, on a few occasions, some electrode stabs entered the region and the opportunity was taken to observe the behaviour of the units isolated.

METHODS

In the stereotactic coordinate system of Sawyer et al. (1954), the brachium is pronounced at a distance of 7-8 mm. behind bregma, 2-8 mm. lateral and 6 mm. below the surface of the cortex. Recordings were most successful when carried out with a Wood's metal electrode because of its superior performance to tungsten when recording from fibres. The electrode tip may be localised during its passage through the overlying tissue by the various characteristic sounds issuing from the monitoring loudspeaker. The cells of the upper cortex, callosal fibres, ventricle and hippocampus all have their own sound. Just beyond the lower region of the hippocampus there is a region in which no electrical activity is picked up by the electrode. When the electrode is pushed down a little further it is possible to hear a slight hiss which can be driven by the movement of small objects in the visual field. Not many units can be isolated in the first descent of the electrode but more are obtained as it is slowly returned to the mid-brain surface. The fact that the electrode had reached the brachium was established histologically in a few cases.

RESULTS

The majority of the units recorded were of similar classes to those of the /

the optic nerve.

1. Small field transient centre-on or -off response. The fields of these units appeared to be slightly larger than those of the equivalent type in the optic nerve (3.0° rather than $2.2-2.6^\circ$). The presence of an inhibitory surround could be demonstrated. The properties were in other ways similar to those of the optic nerve class I.

2. Maintained concentric units. Both on and off types of unit were found with a variety of time constants for the dynamic phase of their response. Many of the units fired spikes in pairs which gave the sound recorded over the monitoring loudspeaker a squeaky quality. Some showed a quite marked dimming response and were difficult to separate from the next group. The field centre size of the units was rather smaller than that of the large field off units.

3. Large field, shadow sensitive units. Half of these units demonstrated surrounds demonstrable by the perimeter spot. These units were similar to those of the nerve although one possessed a pure off centre larger than any recorded from that region (10°). [REDACTED]

4. Directional units. Identical to those of the optic nerve.

5. Large field on-off type. This class of unit was not encountered in the optic nerve. The fields of the three such units recorded were circular and $8-9^\circ$ in diameter. One unit showed an on-off response when stimulated with a perimeter light spot but its maintained activity was inhibited by a black disc entering its field against a white background. One unit was sluggish in its response to movement but the other two were very similar in behaviour to the large field off type and may have been aberrant members of that group.

6. Long field unit. These units all showed spontaneous activity and were very sensitive to movement. The response to slow movement at a constant rate was most pronounced. The units showed an off response and an inhibition of the spontaneous [REDACTED] activity at on. The fields were /

were up to 90° long and were about 20° wide. A surround could not be detected.

7. Quadrant and Hemifield units. Amongst the brachial fibres at the most anterior edge of the superior colliculus, a number of very characteristic fields were found which occupied one quarter or one half of the visual field projection on to a plane. The peripheral boundary of the fields appeared to be co-extensive with the peripheral field of the animal. The other boundaries ran exactly along either the vertical or horizontal meridian, or both. All of these units showed spontaneous activity and the firing rate was extremely constant. The response of the units was on-off all over and they were very sensitive to the movement of objects contrasting with the background. The units were sensitive to a wide range of stimulus movement velocities (0.25° to 100° sec. were effective).

TABLE. Number of units in each category as a percentage of the total number recorded from the brachium of the superior colliculus

		no.	%
Small field transient response	on	2	5
	off	5	12.5
Concentric maintained	on	3	7.5
	off	7	17.5
Large field shadow sensitive	off	9	22.5
Large field	on-off	3	7.5
Long field		3	7.5
Quadrant and Hemifield units		4	10.0
Directional		4	10.0
Total		<u>40</u>	<u>100.0</u>

ANATOMY OF SUPERIOR COLLICULUS

The superior colliculus is the homologue of the optic tectum which subserves the main visual functions in the submammalian vertebrates. The density of primary optic terminations in the superior colliculus and the size of the organ has, in general, decreased as the geniculo-striate has increased in importance. The complexity of organisation of the superior colliculus and its great variety of afferent and efferent fibre connections bear witness, however, to the improbability of it being, as is often claimed, a vestigial organ in even the primates.

The dorsal projection of the superior colliculus in the rabbit lies from the eighth to the sixteenth mm. behind bregma in the anteroposterior plane and from one half to five and one half mm. in the mediolateral plane. The level of the collicular surface is variable but lies, in general, from two to five mm. below the cortical surface.

The nomenclature of Huber and Crosby (1943) is used in the subsequent section for the description of the laminae of the superior colliculus. From the surface downwards the layers are:-

I. Stratum Zonale. This is a narrow layer of fibres amongst which lie flattened marginal nerve cells. May contain cortical and/or retinal projections.

II. Stratum Griseum Superficiale. The optic fibres enter this layer after having turned upwards from the subadjacent stratum opticum and arborise amongst the small and medium sized cells. According to the observations of Cajal (1911), in the rabbit the outer portion of this layer contains fusiform tangentially orientated cells of considerable field size amongst which are small cells with a complex bushy dendritic tree. The more central cells are fusiform but the long axis is radially orientated. The whole of the S.G.S. contains terminations of optic tract fibres but only the lower regions contain corticotectal afferent arborisations.

III. Stratum Opticum. This is the stratum medullare superficiale of Winkler and Potter's rabbit atlas (1911). The upper portion of the layer /

layer consists mostly of fibres which originate in the retina and turn up to the S.G.S. According to Lund (1966) these fibres spread throughout the whole of the S.O. The incoming corticotectal fibres are confined to the lower regions of the stratum opticum from which the majority turn down to arborise in the stratum griseum intermediale. Many incoming cortical fibres appear to enter directly into this lower layer and the S.O., stratum griseum intermediale and stratum album profundum were described as the zone ganglionnaire ou des fibres horizontale of Cajal. The stratum opticum contains a large number of radial fibres which are the axons of the S.G.S. penetrating to the subadjacent layers.

IV. Stratum Griseum Intermediale. The dendrites of large cells in this layer extend upward into the superficial grey. The layer is supplied by the tectal commissures as well as by the two adjacent fibre layers. The deeper fibre layers send up afferents from the parietal or prestriate cortical region (Lund, 1966). The principal efferent fibres of the colliculus stem from this layer.

V. Stratum Album Intermediale. This is the stratum medullare intermediale according to Winkler and Potter (1911). The layer receives fibres from the prestriate cortex, inferior colliculus and is the site of termination of the spino-tectal path (Huber and Crosby, 1943).

VI. Stratum Griseum Profundum.

VII. Stratum Album Profundum. Major efferent path from the colliculi. Little is known of the function of the above layer.

Most neuroanatomists do not include the periventricular layers within the colliculi so that the total number of layers stands at seven, all of which are clearly defined in the rabbit.

AFFERENT FIBRES

The regions of termination of the incoming optic, striate cortico-tectal, pre-striate cortico-tectal and spino-tectal fibres have been mentioned above. Certain other, less well marked, tectal afferent systems have been observed.

The /

The inferior colliculus sends fibres into the deep superior colliculus and terminations have been observed in the S.G.I., S.A.I., S.G.P. and S.A.P. Auditory responses can often be obtained from the cells of these layers (Tarlov & Moore, 1966).

Altman (1962) observed a projection from the lateral geniculate pars dorsalis to the superior colliculus. The results of Cragg (1962) might be interpreted as supporting the presence of such a tract in the rabbit but the nearness of retino-collicular fibres to the damaged region of the LGN casts doubt on the findings.

Altman (1962) records that the pulvinar projects a few fibres to the superior colliculus in the cat but it is not known whether this is the case in the rabbit.

EFFERENT FIBRES

The efferent fibres of the superior colliculus are usually considered to form two groups, the ascending and the descending paths.

Ascending Paths. Tarlov and Moore (1966) describe prominent medial and lateral ascending fibre fascicles from the superior colliculus. The lateral fibres pass to the parabrachial region, supragenulate pretectal nucleus and to the posterior complex which includes the dorsal medial geniculate nucleus. Unlike Cragg (1962), in the rabbit, and Altman and Carpenter (1961), in the cat, they were not able to demonstrate a projection to the pulvinar. No fibres were seen to innervate the dorsal geniculate body from the optic tract but a discreet bundle passed into the ventral nucleus to terminate on a group of fusiform cells. This projection was noted by Cragg (1962) in the rabbit and Altman and Carpenter (1961) in the cat.

The medial ascending fibres run from the superior colliculus into the pretectal area. Preterminal degeneration is traceable to the pretectal nucleus, the pretectal area and the medial and lateral nuclei of the optic tract after lesions to the superior colliculus.

Cragg (1962) has observed the lateral fibres to spread to the ventral reticular /

reticular nucleus and to pass on to the chiasma where they crossed in the commissure of Gudden and ascended to the reticular nucleus. Tarlov and Moore are unsure of the destination of these fibres but claim that they originate from the rostral colliculus (1966).

No direct fibres from the colliculus to the oculomotor nuclei have been traced in the rabbit (Tarlov and Moore, 1966; Cragg, 1962) or cat (Altman and Carpenter, 1961). Such fibres have been demonstrated in the monkey by the use of the Marchi technique (Crosby and Henderson, 1948).

Neither Cragg (1962) nor Tarlov and Moore (1966) were able to convincingly demonstrate centrifugal fibres in the optic nerve after lesions to the superior colliculus.

Descending Paths. Altman and Carpenter (1961) give an account of the descending paths of efferent fibres from the cat colliculus which differs little from the description of Papez and Freeman (1930) for the rat. The subsequent account is based upon organisation of the cat pathways which probably resemble closely the paths of the rabbit.

Predorsal bundle and tecto-spinal path.

Fibres forming this bundle originate in the deep layers of the colliculus and pass ventral to the medial longitudinal fasciculus. It was possible to trace fibres from this bundle to the interstitial nucleus of Cajal and the nucleus of Darkschewitsch. The degeneration in these nuclei was bilateral and they were supplied on the contralateral side by the commissure of the superior colliculus. The majority of the fibres of this bundle terminate in the medial pontine reticular formation. The continuation of the predorsal bundle into the spinal cord is known as the tecto-spinal tract. In the cat the path is not well developed and can be traced down to about C₇ (Rasmussen, 1936). The tract is entirely crossed.

Intermediate tecto-reticular path.

This group of fibres originates diffusely in the deeper layers of the colliculus and projects bilaterally, but predominantly ipsilaterally, on to the dorsal part of the mesencephalic reticular formation.

Tectopontine /

Tectopontine bundle.

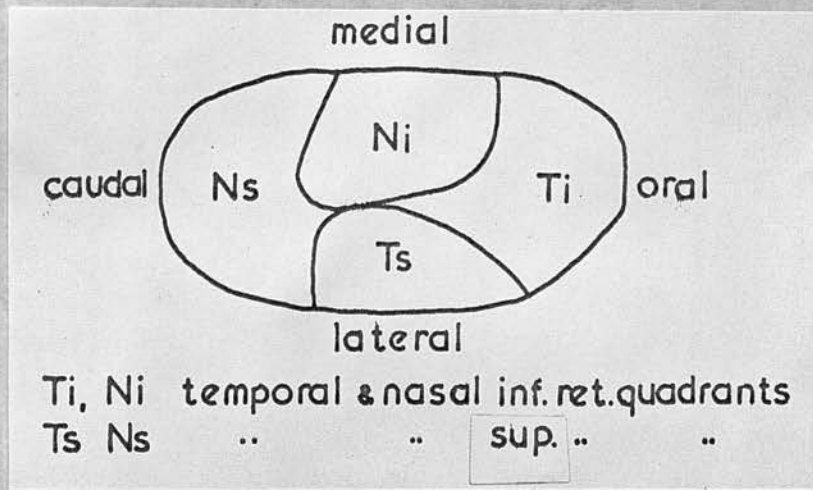
This group of fibres form the largest descending fasciculus. The fibres pass caudal ventrolaterally to the colliculi. The group terminates in the dorsolateral pontine nucleus. The tract has been described in the rabbit by Muenzer and Wiener (1902). Brodal and Jansen (1946) have demonstrated the projection of the dorsolateral pontine nuclei on the vermal cortex of the cerebellum in the region from which responses to photic stimuli may be recorded (Snider, 1950).

Altman and Carpenter (1961) emphasise that the major part of the collicular descending projection is to the reticular formation. The mesencephalic region is supplied by both crossed and uncrossed fibres but the former predominate while in the pons and medulla the tectoreticular fibres are entirely crossed. According to Jefferson (1958), the stimulation of the superior colliculus produces EEG activation and behavioural arousal.

RETINAL REPRESENTATION ON THE SUPERIOR COLLICULUS

INTRODUCTION

The topography of the retinotectal projection was first determined in the rabbit by Brouwer et al. (1923) and then confirmed by Overbosch (1927). Localised retinal lesions were made and the degenerating optic nerve fibres were traced back to the colliculus by means of the Marchi stain. The four retinal quadrants are projected, according to Brouwer, in the following fashion -



The results do not agree with those determined electrophysiologically but the error is not great when it is considered that the method does not show the actual sites of fibre termination.

An electrophysiologically determined map of the projection of the visual field on to the superior colliculus of the rabbit was first obtained by Hamdi and Whitteridge (1953) but only the approximate positions of the meridia were located. Seneviratne (1963) repeated the work using tungsten electrodes to pick up the multiunit responses to a neon light flashing in the visual field of the animal.

Seneviratne found the surface of the superior colliculus to be devoted to the representation of a band shaped region of the visual field of the contralateral /

contralateral eye. The band, which corresponds with the projection of the visual streak into the field, extends along the horizontal axis for nearly 180°. The nasal field is represented on the anterior end of the colliculus and the temporal field at the caudal end. The visual field above and below the horizontal is represented for a total of about 50° on the vertical meridian. The upper field lies medial.

In the presentation of his results, Seneviratne (1963) states that the anteroposterior and transverse diameters of the colliculus are roughly similar and consequently that any distortion of the visual field projection which does not appear in both the horizontal and vertical meridia must result from the deviation of a greater distance of brain surface to the representation along one axis than along the other. This argument is followed by a set of magnification factor studies which purport to confirm the impression, gained from examination of the map of the visual field projection on to the colliculus, that the visual streak is given an expanded vertical representation relative to the more peripheral regions and that along the horizontal the projection is more uniform.

An examination of the original protocol for the magnification factor studies shows, however, that the factor has not been properly derived. Daniel and Whitteridge (1961) define the magnification factor as the distance along the brain surface between two points whose projection into the visual field subtends one degree at the eye. Seneviratne has used distances measured along the plane projection of the collicular surface. No correction for the effects of the collicular surface curvature on the planar projection map of the visual field will thus have been introduced.

It may readily be seen, by reference to some serial sections, that, contrary to Seneviratne's assumption, the collicular surface curvature is not the same along the projection of the horizontal and the vertical meridia and, in fact, differs mediolaterally from anterior to caudal regions. The rabbit brain atlas of Monnier and Gangloff (1961) illustrates this point.

In view of these doubts it was decided that the retinal projection on to /

to the colliculus would be redetermined and a map constructed, by the use of serial sections, which showed the actual distance along the collicular surface between the electrode insertions.

METHODS

Tungsten electrodes were used to record multi and single unit responses of the upper regions of the superior colliculus to small card discs moved in the contralateral visual field of the preparation. The final localisation of the receptive field centre was carried out with the light spots generated by an 'Airmark' projection perimeter. A card bearing a record of the positions in the visual field corresponding to each point of insertion of the electrode is obtained from the perimeter. The polar coordinate system, in which the results are supplied by the perimeter, did not appear appropriate to the rabbit system with its visual streak and the results were plotted in a system of parallels and vertical meridians. The position of the optic nerve head and myelinated band projection into the visual field was noted for each experiment and, during the transposition of the coordinates, the maps were transformed to a standard condition in which the optic nerve head projected about 20° below the horizon and the streak was arranged horizontal .

After fixation, the superior colliculus was sectioned and stained. Each section was projected by means of a photographic enlarger on to a piece of paper and a $\times 10$ drawing was made of the collicular surface and of any electrode insertions apparent. A map was then constructed showing the position of the electrode insertions in terms of mediolateral distance along the collicular surface. About 80% of the electrode insertions were identified in this fashion. Enough were recovered to establish the relation between the sections and the matrix of electrode insertions recorded from the stereotactic machine. No attempt was made to correct for anteroposterior curvature because the rabbit colliculus is predominantly flat in this plane and curvature is marked only at the extreme front and rear.

The new coordinates allocated to each electrode insertion were marked on /

on the map showing the actual distances on the collicular surface between insertions, and the desired meridia were drawn in.

RESULTS

The variation in the visual field projection on to the colliculus of different rabbits is quite marked but in no case were the horizontal and vertical meridia in a position corresponding to that determined by Brouwer et al. (1923). The plane projection maps are in essential agreement with those of Seneviratne. No ipsilateral projection was recorded.

The most complete version of the reconstructed maps is shown in figure 56. It is clear that, even after the correction for surface curvature, the streak region reveals an expanded representation in the vertical plane compared with the horizontal. The interval between the meridia along the horizontal axis is uniform as was described by Seneviratne.

A quantitative description of the visual field projection on to the colliculus is obtained by the use of the magnification factor, M , which was introduced by Daniel and Whitteridge (1961). This parameter is described as the distance in mm. separating the projections, at some level in the visual pathways, of two points which subtend an angle of 1° at the anterior nodal point of the eye. The measurements must, of course, be derived from flattened maps of regions presenting a curved surface. For comparison with the ganglion cell count we include plots of the magnification factor's values along the vertical meridian which passes through the optic nerve head, and the parallel which projects on to the peak of the ganglion cell count in the visual streak (fig. 58). In the vertical, the magnification factor ranges from $0.05 \text{ mm}/^\circ$ to $2.3 \text{ mm}/^\circ$. Along the horizontal it is remarkably constant at about $0.035 \text{ mm}/^\circ$. The temporal meridian shows a rather lower peak value of vertical magnification factor than the nasal.

DISCUSSION

The peak value of vertical magnification factor ($2.3 \text{ mm}/^\circ$) is somewhat greater /

greater than that determined by Seneviratne and Kerr (1963) for unflattened collicular projection maps ($1.6 \text{ mm}/^\circ$). The horizontal values are in agreement for Seneviratne et al. quote $0.035 \text{ mm}/^\circ$ compared to the $0.035 \text{ mm}/^\circ$ described above. It thus appears that the vertical expansion in the nasal representation which is revealed in the maps of Seneviratne (1963) is a real feature of the collicular map and does not result from the effects of surface curvature on a uniform representation.


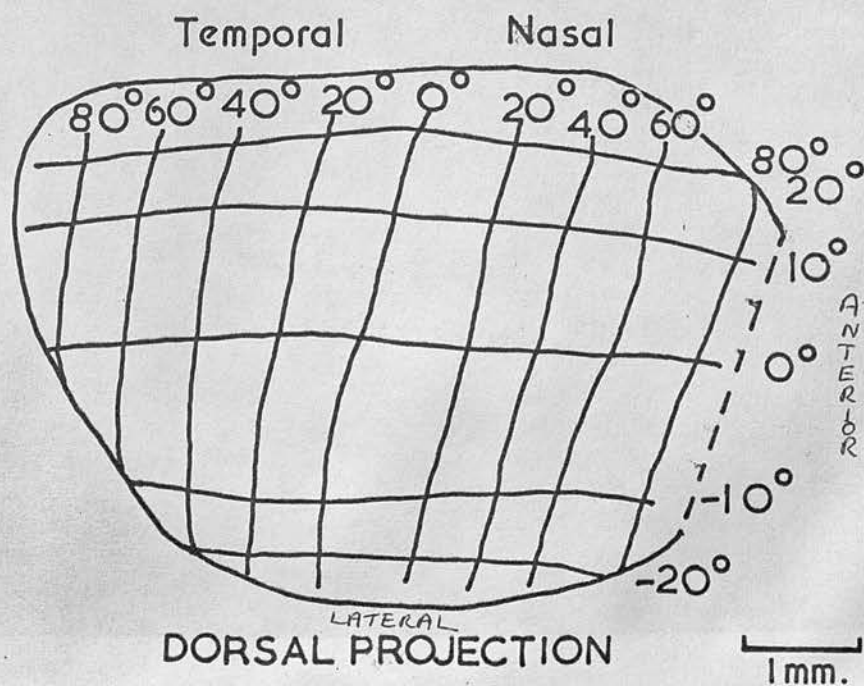


Fig. 56

Fig. 56 A. Both maps are of the right superior colliculus with the upper visual field represented along the medial margin of the organ and the frontal field along the anterior margin. The meridia run from top to bottom of the map and the parallels across. The upper field parallels have positive and the lower field negative coordinates.

B. Dorsal projection and reconstructed, flattened map from another animal showing a similar arrangement to that of fig. 56A, (note difference in scales). The increase in vertical magnification in the nasal region in this fig. is found in some cases but not in others and confirms Seneviratne's maps. The numbers above the dorsal projection map of fig. 56B designate the rows of electrode insertions marked as black spots on the map.

A



B

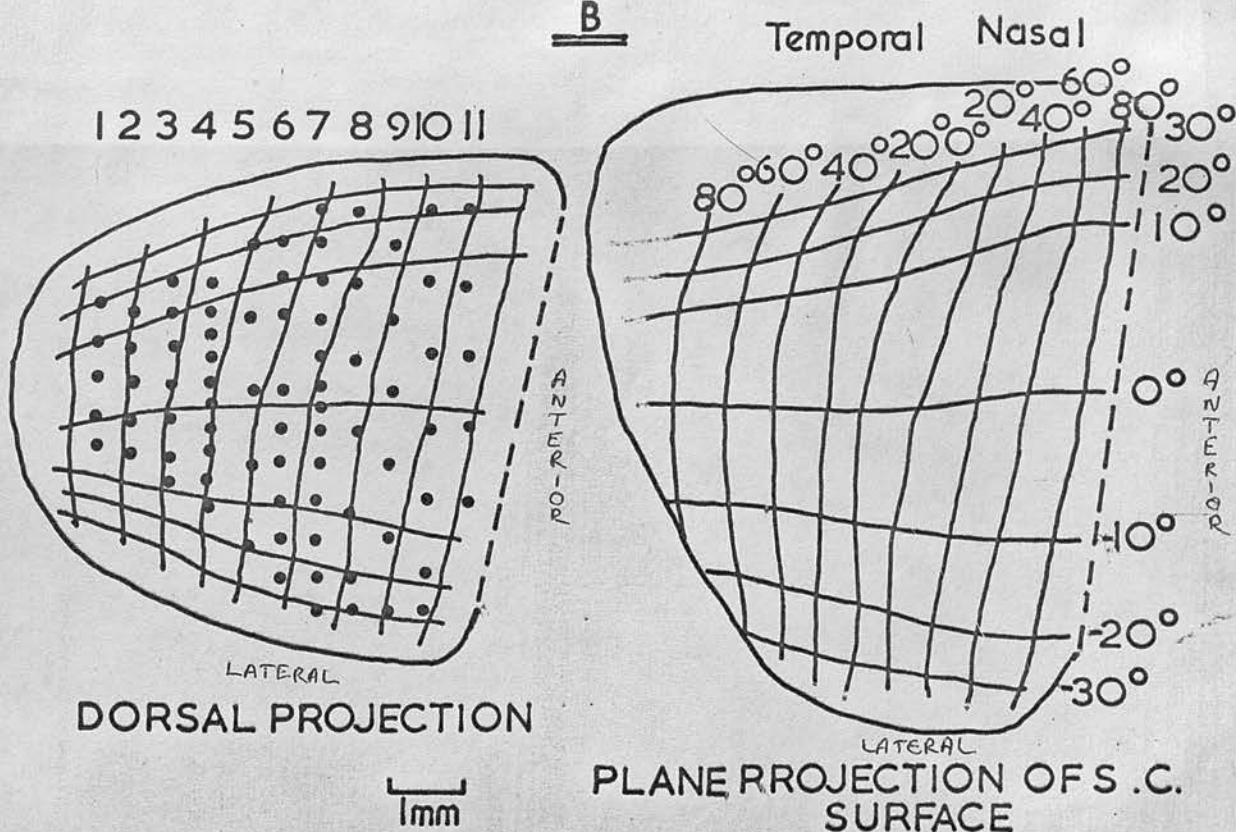


Fig. 57 This diagram shows the coordinates in the visual field of each of the points marking an electrode insertion in fig. 56B dorsal projection map. The numbers above each line of points in the visual field correspond to those above each row of electrode penetrations in fig. 57B. The most medial points on the colliculus correspond with the most elevated in the receptive field. Successive points encountered in moving laterally on the colliculus and inferiorly in the visual field correspond.

SUPERIOR COLLICULUS

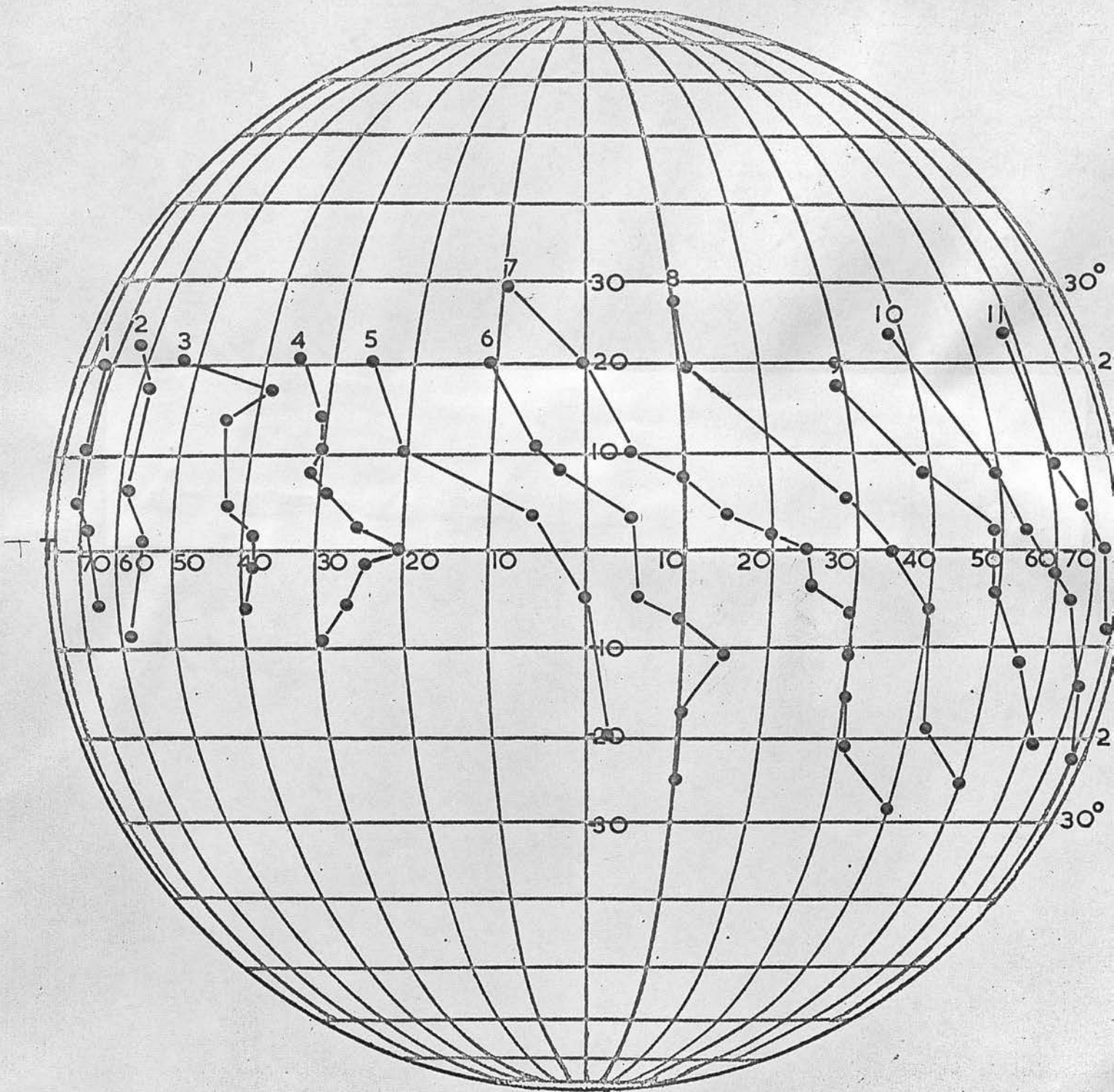
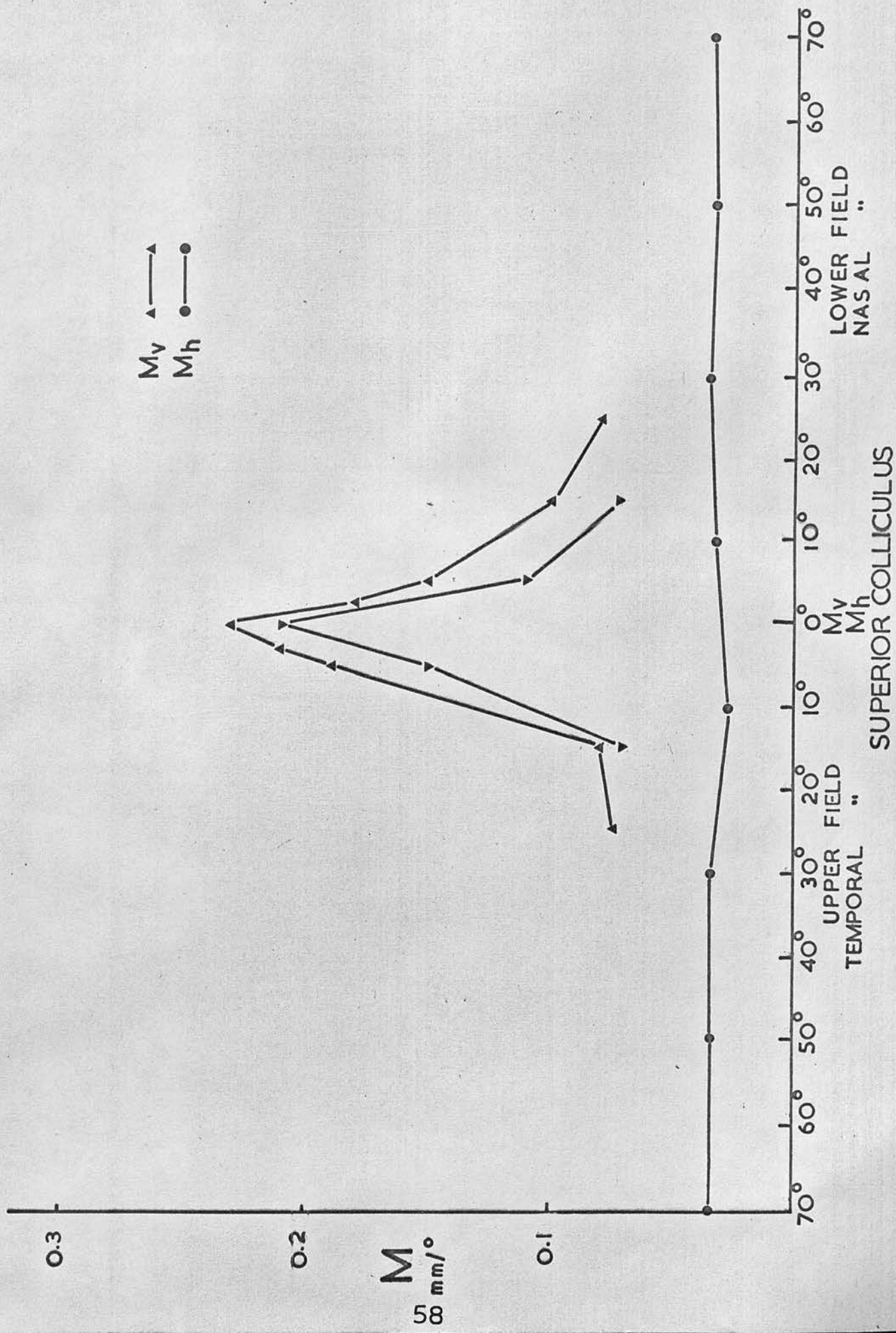


Fig. 58 Plot of the absolute vertical and horizontal M factor ($\text{mm}/^\circ$) for various regions of upper and lower or nasal and temporal visual field projection on the surface of the superior colliculus. The horizontal and one of the vertical plots are from the same animal. All three plots were taken from flattened maps. The vertical magnifications were obtained by averaging intermediate parallels across the visual field projection and determining their spacing.



SINGLE UNITS OF THE SUPERIOR COLLICULUS

METHODS

The majority of the electrode insertions that were carried out for the purpose of recording single units from the superior colliculus were made into the region bearing the central portion of the upper visual field projection. This limitation was accepted in order to ensure that the electrode penetrated the organ at right angles to the laminae. It was thus possible to compare the depths at which the different types of unit were encountered in various insertions. A histological investigation of the electrode tracts confirmed that quite accurate estimates of the layer from which a given unit is recorded may be made by referring the depth reading to that of the collicular surface as determined when the electrode is being removed from the brain. In this fashion errors resulting from dimpling are avoided. The adequacy of this method is supported by the findings of Vejbaesya (1967) but not by those of Gaze and Jacobson (1964).

When an electrode is in the space above the colliculus, but is not actually touching the surface, it is possible to record a massive polyphasic response when a small stimulus is moved at a sharply localised region of the visual field. Large stimuli, greater than 10° wide, are not effective and in some preparations it might be possible to overlook the response to waving of a hand. As soon as the surface is touched it becomes possible to hear the sharp crackle of the axonal and cell action potentials when stimuli are presented. The upper regions of the colliculus do not show much spontaneous activity under light urethane anaesthesia.

Wood's metal and tungsten electrodes were found to be equally effective for recording units in the superior colliculus. The wide barrel of the former causes considerable damage to overlying cortex, some of which is striate with projections to the colliculus, so that the latter were preferred.

RESULTS

Multiunit evoked response. The upper 0.6 mm. of the colliculus gives a marked multiunit evoked response to the flashing of a small light spot in the /

the appropriate part of the visual field. The off response is particularly noticeable because of its oscillatory form and long decay time (6 sec.) (fig. 59a). The movement of small (1°) card stimuli produces an equally marked multiunit response (fig. 59b) but larger forms ($10^\circ+$) were much less effective. Large shadows were better stimuli than large card forms with well defined edges.

A detailed examination of the multiunit evoked response properties reveals the presence a well developed lateral inhibitory phenomenon. Flashing of a 1° light spot (fig. 59c) gives rise to a prolonged reverberatory off response and a more abruptly terminating on response. When the light spot is 4° in diameter, the off response is considerably reduced (fig. 59d) while at whole field off the on and off responses are similarly abrupt (fig. 59e).

The multiunit response shows a well developed dimming and some brightening response over the range from 0.1 to 150 lux of screen illumination (fig. 60a,b). The gross response will synchronise with the rapid movement of small card stimuli or with flickering shadows in a restricted region of the visual field (fig. 60c).

The region from which the multiunit response is recorded corresponds with the stratum griseum superficiale in which there are a number of cell types as well as the well developed terminal arborisations of optic nerve fibres. The properties of the collicular surface response show a marked resemblance to those of the large-field off units of the optic nerve (class 4). Such units were noted as being present in the brachium of the superior colliculus and would necessarily project to the stratum griseum superficiale. An examination of the unit types in the colliculus was undertaken in order to determine whether such projections existed and a general description of the collicular unit characteristics.

Units in the upper 0.8 mm. of the colliculus.

Off units. It has been found possible to record only relatively small field off units from the upper 0.2 mm. of the collicular surface. The units showed spikes of very small amplitude which were difficult to isolate from the multiunit response and which possessed the characteristics of /

of a fibre response. The surround is well developed and latency to a 1° spot was 40-50 msec. Maintained activity was not common. The units were difficult to hold and their properties were more readily studied by ear than by viewing on the oscilloscope screen.

Below, and sometimes amongst, the above units it was possible to isolate large amplitude spike potentials, up to 1 mV, which possessed a predominantly off centre field about 4° in diameter. Even a $\frac{1}{2}^\circ$ light spot at the field centre elicited a slight on response when flashed. Some of the units showed a clear prepotential in the spike or gave an injury discharge at the termination of recording and were thus identified as cells. Figure 6/a shows the response of such a unit to the flashing of a 1° light spot. In the transition from 1° spot to 3° , 10° and finally to whole field illumination (fig. 6/ , a, b , c) there is a marked decrease in the transient off response and an increase in the on response. The response at off is maintained while that at on terminates abruptly. The units give a marked dimming response to a 1° spot (fig. 6/d) which is reduced if the whole field is illuminated. The firing readily falls into synchrony with the rapid movement of a small object or shadow in the receptive field. Large shadows are better stimuli than large card forms.

On-off units. It was mentioned in the above section that the collicular large field off units showed a slight on response to even $\frac{1}{2}^\circ$ spot flashed in the field centre. In the deeper parts of the stratum griseum superficiale, 0.5-0.8 mm. down, the units possess more pronounced on responses and are, for the most part, classified as on-off units, a category in which the more superficial units should strictly be included. The field centre varied in size from 0.5° to over 10° in diameter. Lateral inhibition was noticeable in many of the units. The majority of the units possessed fields of less than 5° in centre diameter and most of these, 50% of the total, were noted as being sensitive to rapid movements.

A number of the on-off units possessed a large, 10° to 15° diameter field in which the distribution of on and off responding regions was rather patchy /

patchy. Some regions responded to on others to off of a light spot and some to both on and off of the exploring light spot. These units were clearly identified as cells by their spike shape. The large field on-off units did not follow rapid movement well and, in more than half of the cases, the fields showed a marked inhibitory surround.

Directional units. A number of directional units were recorded towards the lower margin of this region. The fields were 2-3° in diameter and their characteristics were similar to those of the optic nerve. The spike shape was never that of a cell. The depth at which the units were recorded suggests that they may have been located in the stratum opticum.

If the region of the visual field which gives rise to the multiunit evoked response is explored with a small stimulus during the descent of an electrode into the colliculus, it is found that the evoked response is considerably reduced in magnitude by the time the electrode has descended some 0.6 mm. into the colliculus. Below this depth it is reduced further and is replaced by a hiss response rather like that recorded from the brachium of the superior colliculus. This has regularly occurred by the time a depth of about 0.8 mm. has been reached and it is to be concluded that the stratum opticum has been reached. It is difficult to get isolation of the fibres in this region, perhaps because they lose their myelin sheaths upon entering from the brachium. Certain units with characteristic properties may be isolated from the hiss by listening to their response but the units do not display well on the oscilloscope screen. Large-field off and directional units have been identified in this fashion. It is usually found that the region of visual field which lies temporal and nasal of that from which the evoked response was aroused will give rise to a hiss response if stimulated by slowly moving objects. This region of the field extends no more than 5° in the vertical but can be up to 20° long. The explanation is not obvious. The response cannot be that of optic fibres alone for it is obtained from a region of visual field, nasal to the projection of the electrode/

electrode insertion, whose representing fibres will have terminated some distance in front of the electrode. These 'hiss wings' develop consistently at a depth of about 0.7 to 1.0 mm.

Units recorded from 0.8 to 1.7 mm.

Long field unit. These units possess fields with a diameter of up to 100° if mapped with a neon flash. The field gives a weak on or on-off response except along a band at the centre. This region is up to 100° long and varies from about 5° to 20° wide in the deeper layers. The band splits the receptive field in half and always runs parallel to the visual streak. The band is more sensitive to movement than the surround and gives a vigorous and predominantly off response to the flashing of a light spot. The band region gives rise to a response of shorter latency (40-50 msec.) than the surround (100-120 msec. at periphery) with the same stimulus (fig. 62a,b).

The response of the band (which gives rise to the description long field unit) is similar to either (fig. 62c,d) a whole field or 2° flash and consists of a massive off and a more restricted on response. The maintained activity is suppressed at on of light illuminating the band region (fig. 62d). If a 5° light spot is flashed at various points ranging from the centre of the band to 30° below (figs. 62e, 63a,b,c), it is observed that the off response is reduced considerably in intensity as the spot is moved further from the band. The response of the band to the movement of a card stimulus falls off much more rapidly. A black 5° disc moved along the band gives rise to a powerful response (fig. 63d) but at only 20° below the band centre the response has almost entirely disappeared (fig. 63e). The response to movement along or across the band is equally readily elicited (fig. 64a,b). The band region gives a good decremental dimming response (fig. 64c) and firing readily falls into synchrony with fast movement. The units vary in their readiness to respond to slow movement along the field. The surround gives no response to movement of card or light stimuli. If spontaneous activity is present, it is usually found to be reduced by whole field illumination.

The /

The latency of these units can be up to 80 msec. Some of the units show prepotentials and / or an injury discharge when the electrode is advanced which was the basis for their classification as cells. The properties of the band region are in many ways reminiscent of those of the large field off units of optic nerve and colliculus.

Units found below 1.3 mm. The previously described group of long field cells falls within this category but the deeper lying examples have been included with the more superficial to form a class with the distinctive properties described above. Apart from the long field units, it becomes increasingly difficult to study and to describe the properties of the units encountered in the deeper layers of the colliculus. The action potentials of the majority of units described subsequently were of long duration and possessed prepotentials. Injury discharge was often precipitated by electrode advance and it was consequently concluded that the majority of the encountered deep units were cells.

Units responding to visual stimuli are mostly confined to the region from 1.3 to 2.6 mm. down from the collicular surface. The long field cells form the largest class in the upper part of this region from about 1.3 to 2.0 mm. down. The remaining units have not been subdivided into classes and will be dealt with together. More than half of these units respond to the flashing of a light spot within the receptive field but the response to moving card stimuli was much better. A few units would respond to fast movement but the majority fired only to slowly moving figures (less than $10^\circ/\text{sec.}$). When mapped out with a light spot or by movement response, the fields are from about 8° to 40° along their major axis. The fields are circular or somewhat oval with the major axis horizontal or vertical. Spontaneous activity was not marked.

Single units recorded from the lower part of this region (1.8-2.6 mm. down) are, in general, much more difficult to isolate. The majority of the units will respond to neither light spot (fig. 65a), whole field (fig. 65b) nor decremental dimming stimuli (fig. 65c). Slow and, more rarely, fast movement

movement will elicit a response (fig. 65d) but this habituates very rapidly in the majority of cells. Figure 65e shows the habituation of a unit to movement of a 5° black card disc through the receptive field. The improvement in the response after a recovery period of 15, 30 & 60 sec. is shown in figs. 66a-66c respectively along with subsequent habituation to repeated presentation of the stimulus.

Some of the units show a greater response to movement of stimuli in one direction which is usually parallel to the horizontal. Detailed examination of the field properties is difficult for regions of the field disappear and return during stimulation.

Some of the units in this layer respond to auditory and tactile stimuli as might be expected in the former since the spino-tectal paths and the inferior colliculus project to the region.

Certain characteristic units were recorded on occasion from about 2.0 mm. to 4.0 mm. below the collicular surface. Histological controls were not made at this depth and efferent tracts may have been encountered. The spikes were of large amplitude while the receptive fields occupied either an entire quadrant or hemisphere of the visual field. The margins of the fields ran along the horizontal or the central vertical meridians and boundaries in no other region were encountered. The responses do not habituate and are sensitive to movement. The response to large stimuli (fig. 67a) is inferior to that generated by small objects (figs. 67b). A few of the cells show spontaneous activity but they do not respond well to the flashing of a light spot (fig. 67c) or rapid movement (fig. 67d).

Unit lamination. The underlying table shows a classification of the recorded collicular single units arranged in the approximate order in which the various types are encountered during an electrode penetration. The number and percentage of each class recorded are shown but little weight should be attributed to the table for it must reflect the ease with which certain types are identified rather than any absolute distribution. Figure 68 indicates the depths at which the various unit types were recorded. Alongside /

Alongside the abscissa is a schematic which indicates the collicular layers as determined from a section taken through the region from which depth measurements were obtained. No correction for shrinkage during mounting was made. The lamination is very marked and probably reflects the layering of cells rather than fibres since it was found to be very difficult to isolate units in the optic stratum which possessed properties like those of the brachium and optic nerve.

TABLE: Number and percentage of each class
of single unit recorded from the rabbit
superior colliculus.

<u>Class</u>	<u>No.</u>	<u>%</u>
Small field off	15	16
Large field off	8	8
On-off	10	10
Directional on-off type	5	5
Long field	22	23
On-off habituating or not	17	18
Movement only, habituating	13	13
Quadrant and Hemisphere	7	7
Total	<u>97</u>	<u>100</u>

DISCUSSION

Literature treating rabbit collicular units. The mammalian superior colliculus has been relatively neglected in the literature on the visual system. A pioneer study of the collicular multiunit response was carried out by Wang (1934) but Hamdi (1953) was the first to describe the change in the evoked potential receptive field as the electrode penetrates the tectum. The multiunit long field response was found in the deep S.G.S. and S.O. In this work, long field units have been found in the S.O. and S.G.I. alone.

Horn /

Horn and Hill (1966) have given an account of units in the tectotegmental region which respond to various sense modalities. Under urethane anaesthesia, 35 out of 87 units were found to respond to photic stimuli. 10% of the units responded to sound, touch and light stimuli, 24% to two modalities and 66% to one sensory modality. The deeper units showed marked habituation. It is clear that the majority of the units were recorded in the regions below the stratum opticum but some multimodality units were obtained from the S.G.S.

A more elaborate classification of rabbit tectal units was set up by Hill (1966). Three major divisions were made. 35% of the units were of homogeneous field ranging from 5° to 77° diameter; 39% were on-off centre concentric types with fields from 4-80°, responding sluggishly and habituating to repeated stimuli; 10% of this group were directional. 26% of the units possessed asymmetric fields which, because of the band dividing their field into two parts, are to be identified with the long field cells described above. No details of lamination are given and none of the types appear to correspond with the collicular large field off units. It appears likely that the multiunit response prevented these authors from studying the properties of the units in the S.G.S.

The most detailed account of collicular units is contained in Schaefer's (1966) report on units recorded from the freely moving rabbit. 42 units were isolated and their positions were marked by means of electrolytic lesions. A description of the unit lamination was thus achieved which confirms the more crude outline of collicular lamination which is given above. Units of the S.O. and S.G.S. are described as responding, in a non-habituating fashion, to the rapid movement of stimuli in all directions and to light spot flashing. The units of the S.G.S. are said, however, to fail to synchronise their firing with the repeated presentation of stimuli at a lower frequency (6/s.) than units of the S.O. (14/s.). The S.G.I. contained both rapidly and slowly habituating units of which less than 50% responded to light flashes. Directional units were present of which the majority responded only to movement along /

along the horizontal. Long field units were not described by Schaefer which suggests that the directional units responding to horizontal movement may be equivalent to the sensitive band shaped region of those units, some of which are located in the S.G.I. The units of the S.G.P. were predominantly sensitive to movement and almost all were directional. Only 16% would respond to a light spot and the majority were rapidly habituating in their response. One very interesting observation made by Schaefer was that directional units of the temporal quadrant are predominantly sensitive to nasal movement and vice versa for the units of the nasal quadrant. Sensitivity to vertical movement was less marked. Units whose receptive fields lay on the central vertical meridian appeared to be sensitive to movement towards nasal and temporal.

Figs. 59 - 67 Superior colliculus unit responses which are described in the text between pages 92 and 98.

SEE general notes following legend of fig. 43.

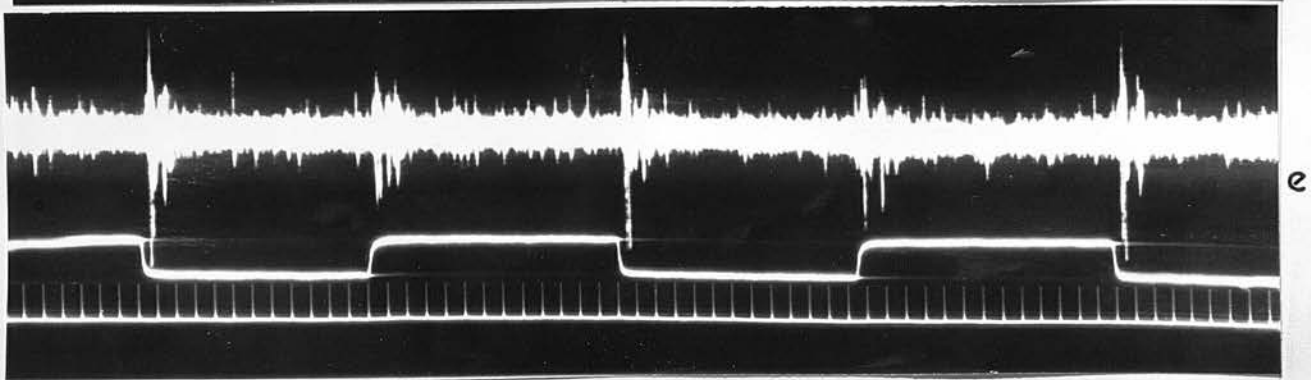
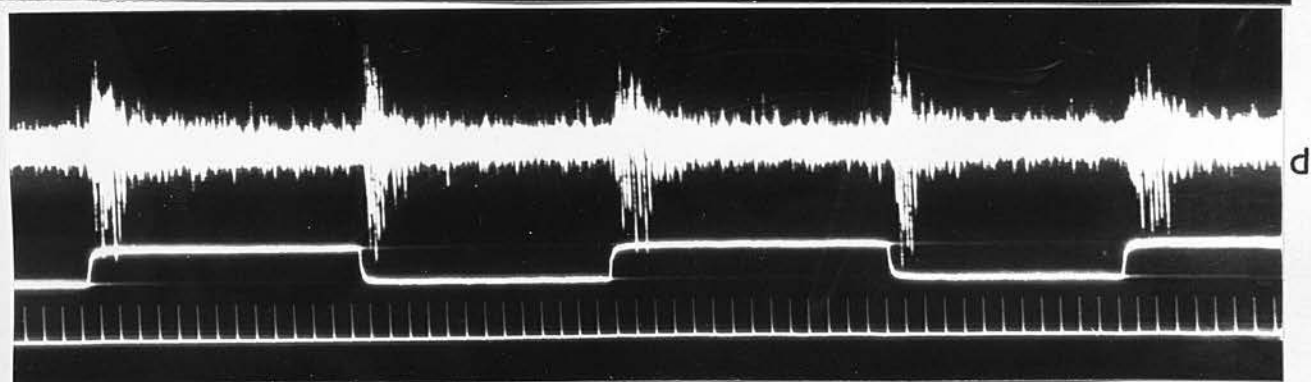
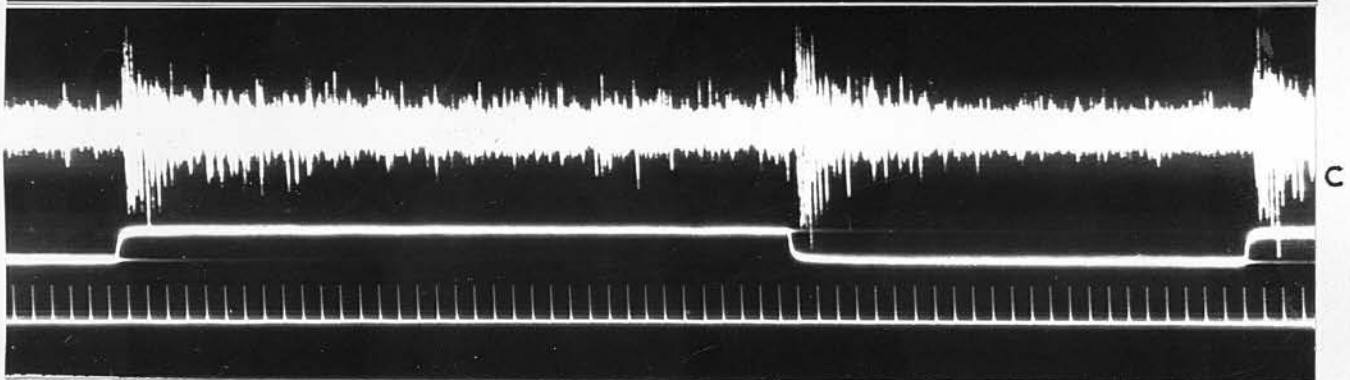
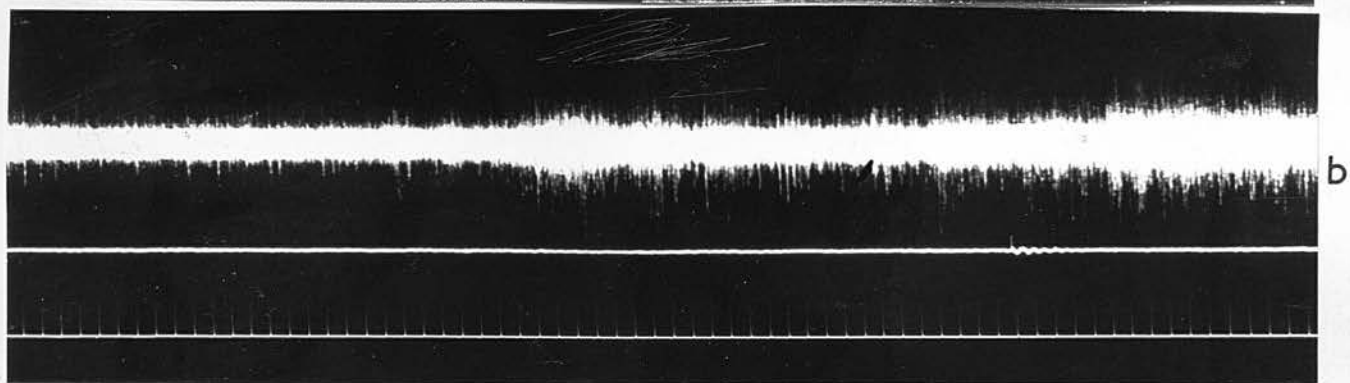
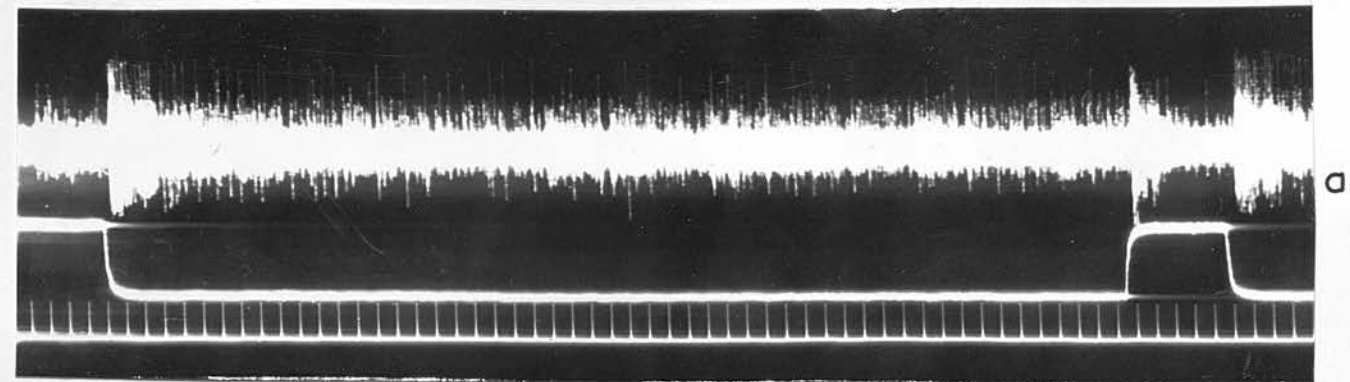
Multiunit response in the upper part of the stratum griseum superficiale in response to the switching off of a 1° light spot appropriately located in the visual field. Compare the prolonged activity during some six seconds of darkness with the abrupt termination of the response to the on of the light spot. The downward movement of the monitor trace indicates off of the light ; upward movement is on .

Multiunit response of the same region to the movement of a 1° diameter card stimulus. Movement begins about half way along the record.

This and subsequent photographs illustrate the presence of lateral inhibitory phenomena in the surround response. The response shown is to off and on of a 1° light spot. There is less background activity during the on period. Down of the trace indicates on and up is off in this and the next three pictures.

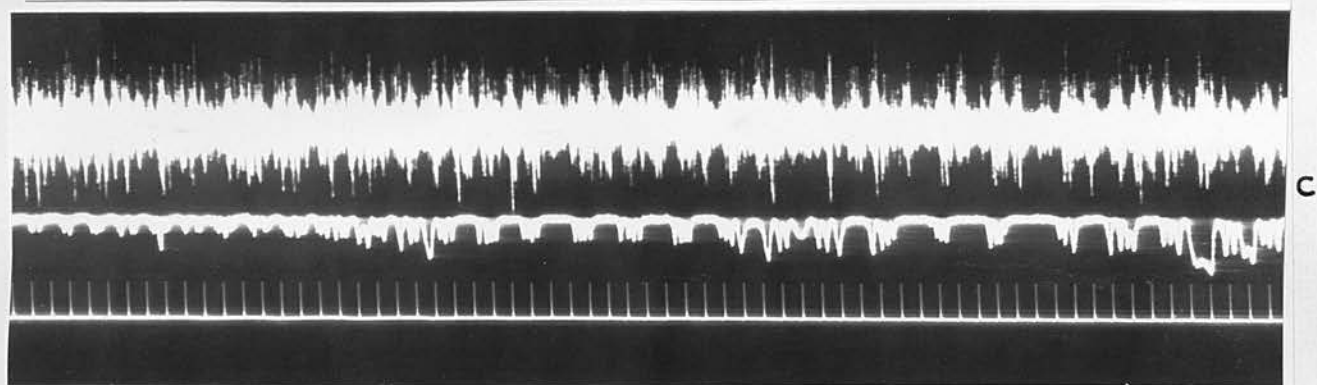
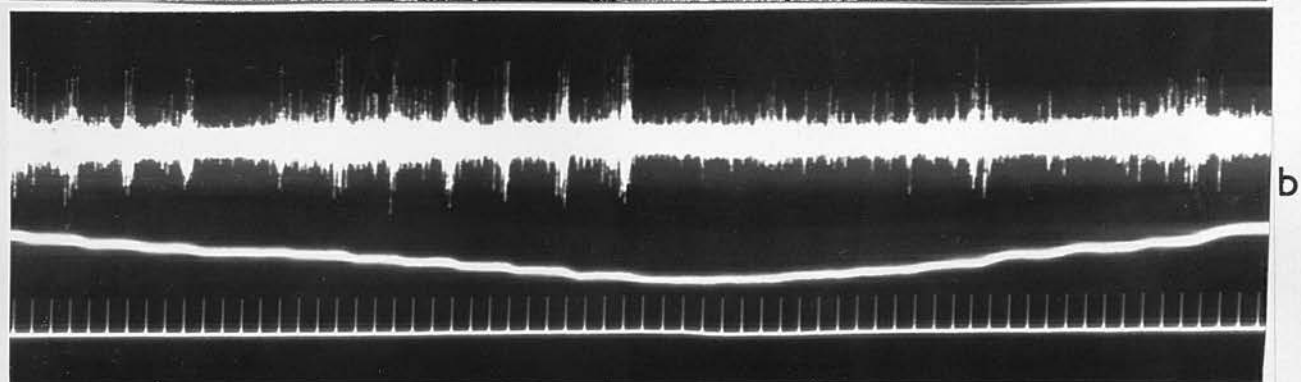
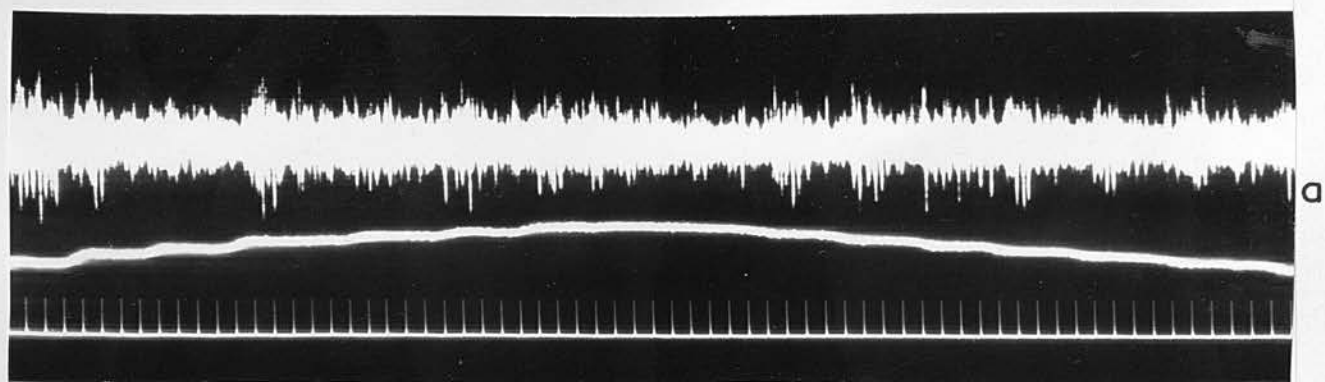
The spot size is now 4° in diameter. Activity at off is considerably reduced. Monitor as above.

Flash of the whole field illumination elicits an on response which is greater than the off response. Monitor as above.



a & b show response of the surface unit population to dimming and brightening of a 5° spot of light. The dimming response is the more marked. The monitor trace shows changes in the light intensity; upward movement of the trace shows brightening and downward movement indicates dimming.

Multi-unit response synchronising with the rapid movement of shadows cast on the receptive field. Downward movement of the monitor trace indicates passage of a shadow in the 5° illuminated area under investigation.



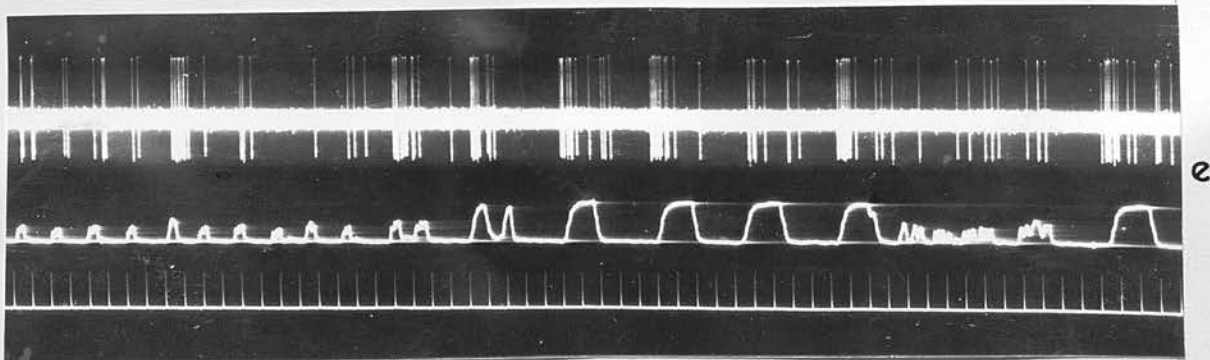
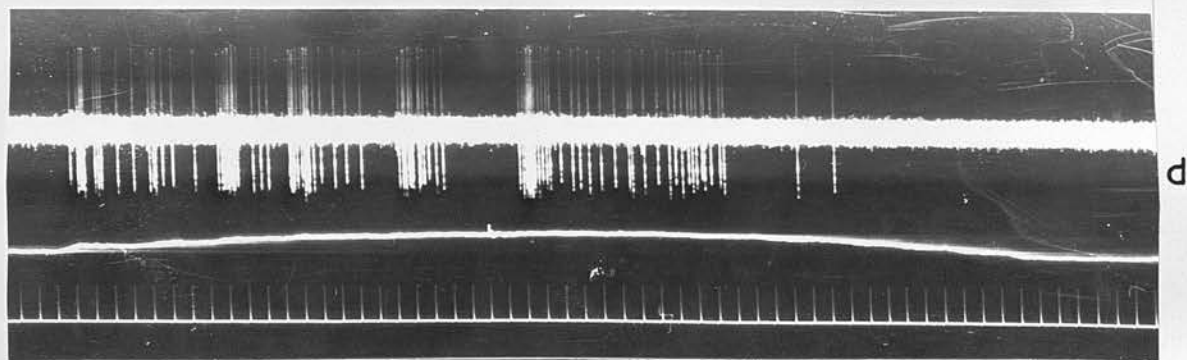
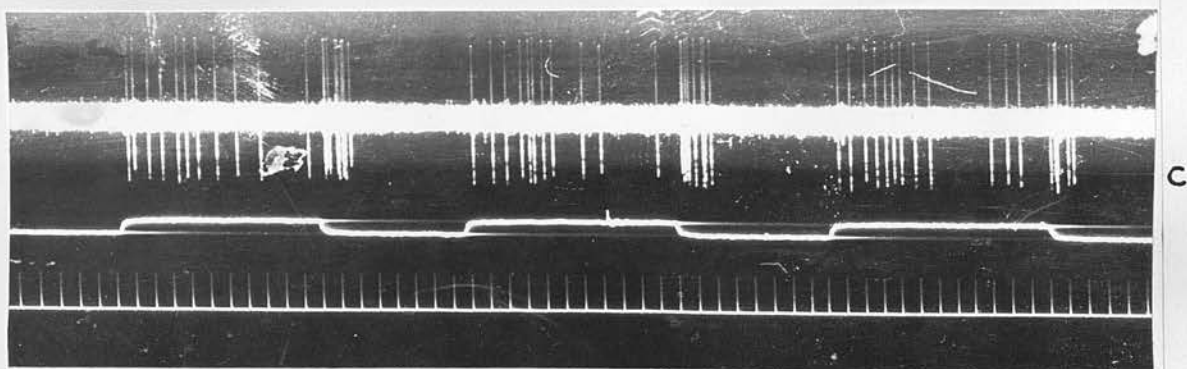
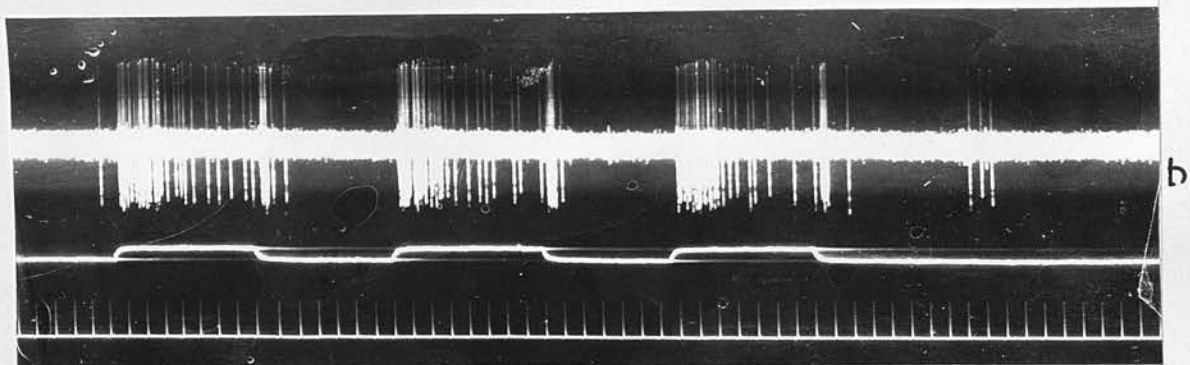
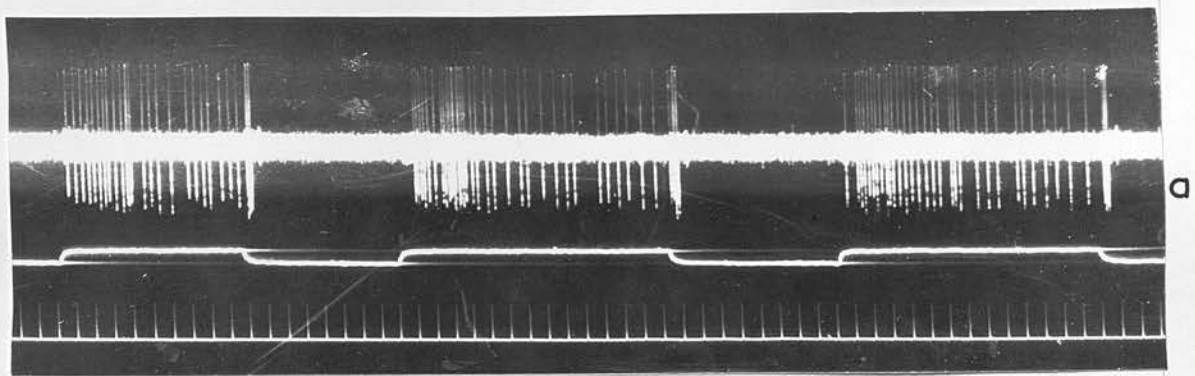
Large field off unit of the stratum griseum superficiale .
1° light spot centred in receptive field elicits a
predominantly off response ;slight on component (which
appears even for 0.5° spot. Monitor trace movement up is
indicative of off of the light in this and other pictures on
this page.

Large field off unit responding to flash of 30° light spot.
Conditions and monitor trace as above.

Large field off unit responding to flash of a 10° light
spot. Conditions and monitor trace as above. Note the
reduction of the off and spreading of the on response as
the stimulus is increased in diameter.

Response to decremental dimming of a 1° light spot . The
response to brightening is absent . Whole field illumination
reduces the off response considerably. Upward movement of th
monitor trace indicates increase in intensity of illuminatio
of the receptive field .

Response of a large field off unit of colliculus to rapid
movement of shadows in the 50° illuminated region of the r
receptive field .



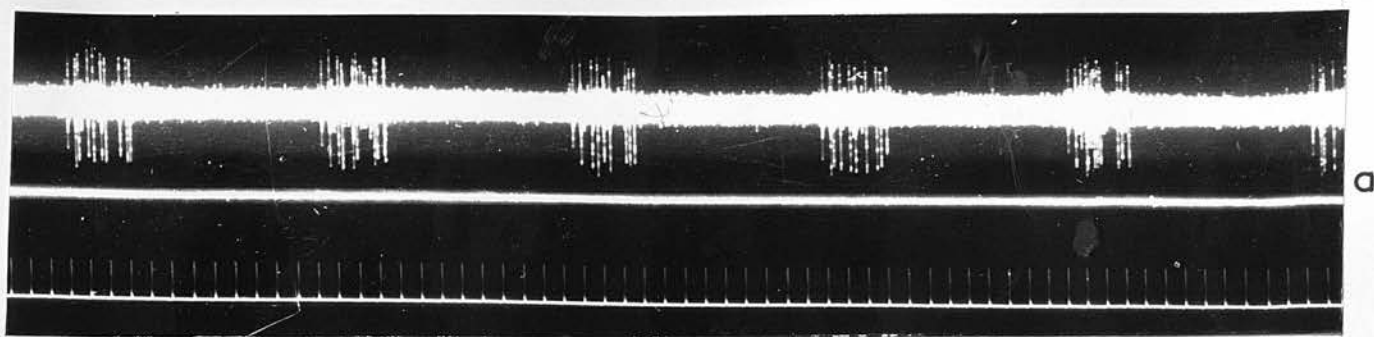
Long field unit of the superior colliculus responding to the presentation of a neon flash at a point on its band shaped field. The first spike of each response to a flash is an artifact indicating the occurrence of the flash. The latency from the band region is thus seen to be about 40 ms.

Response from the surround of the above unit . The conditions are otherwise similar and latency is seen to be about 100 ms.

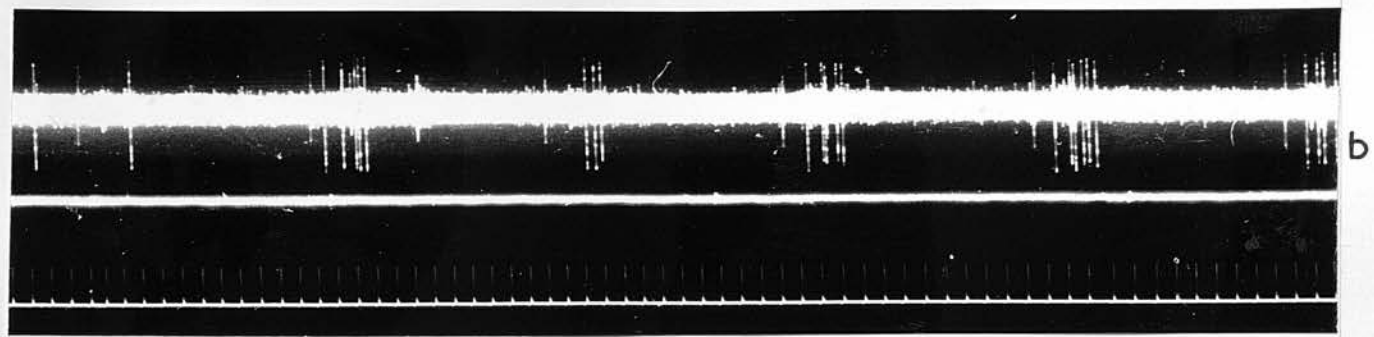
Response of long field unit to a whole field light flash. Up of the trace indicates off of light .

Response of a long field unit to a 2° spot centred on the band region . Up of the monitor trace indicates off of the light .

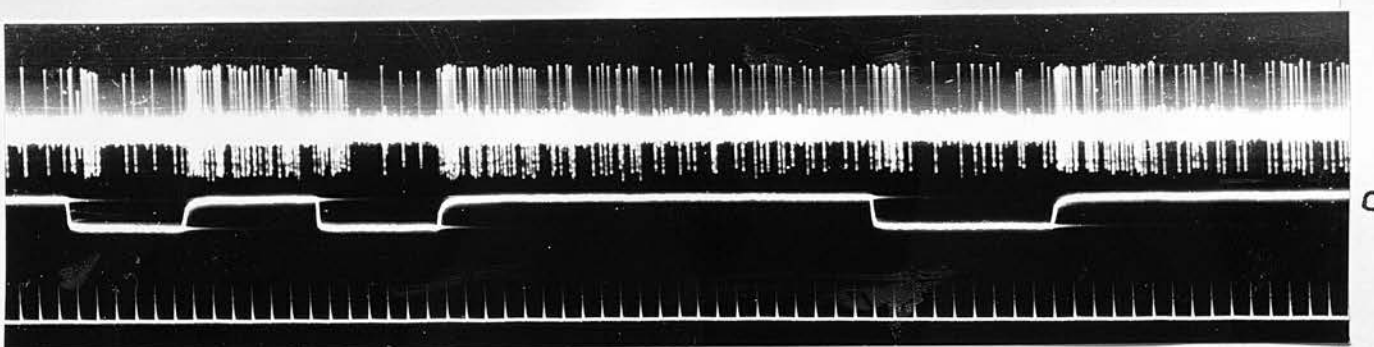
Response of another long field unit to the flashing of a 5° light spot centred on the band region of the receptive field. Up of the monitor trace indicates off of the light.



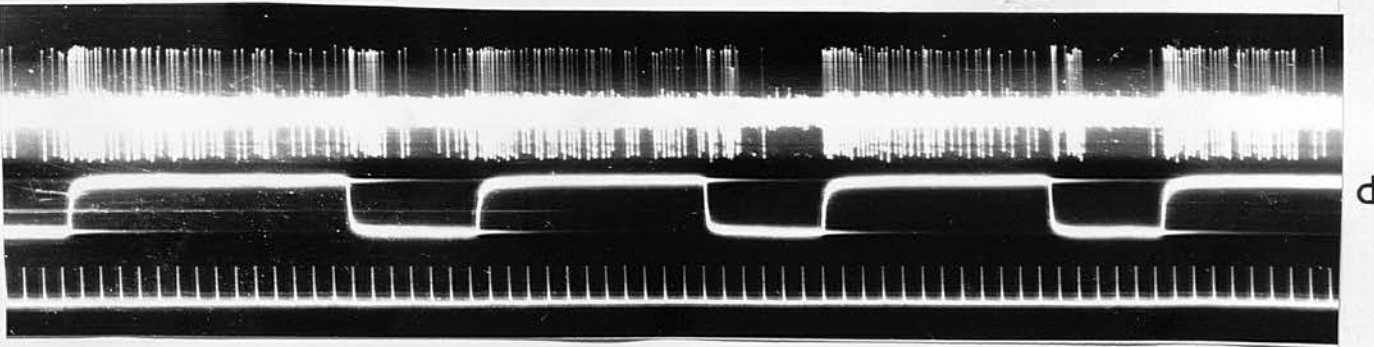
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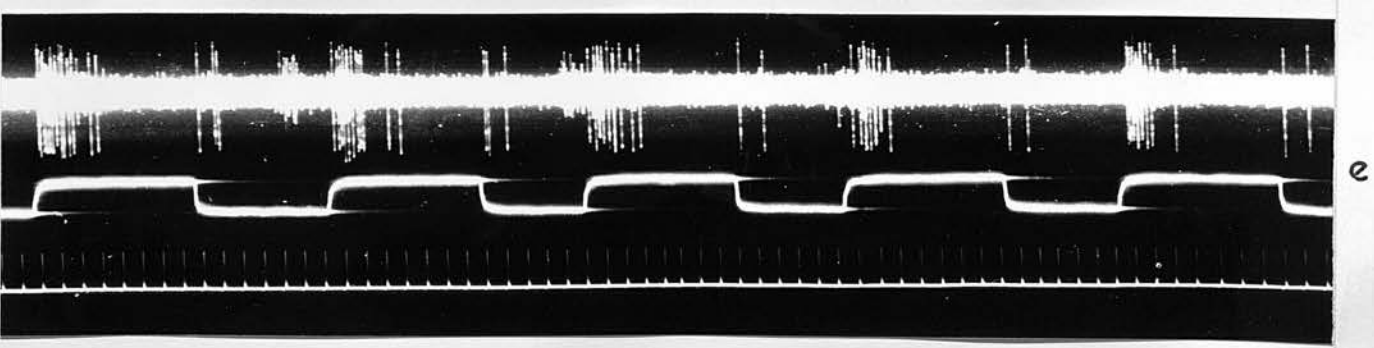
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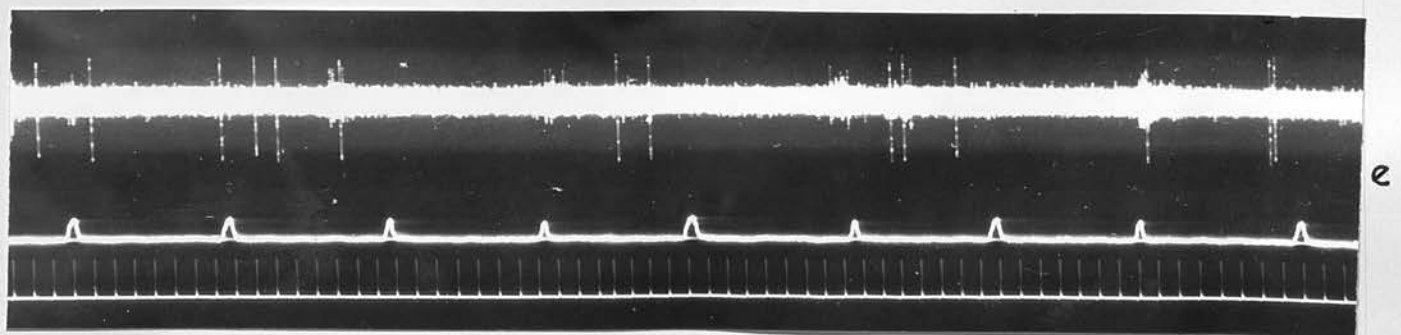
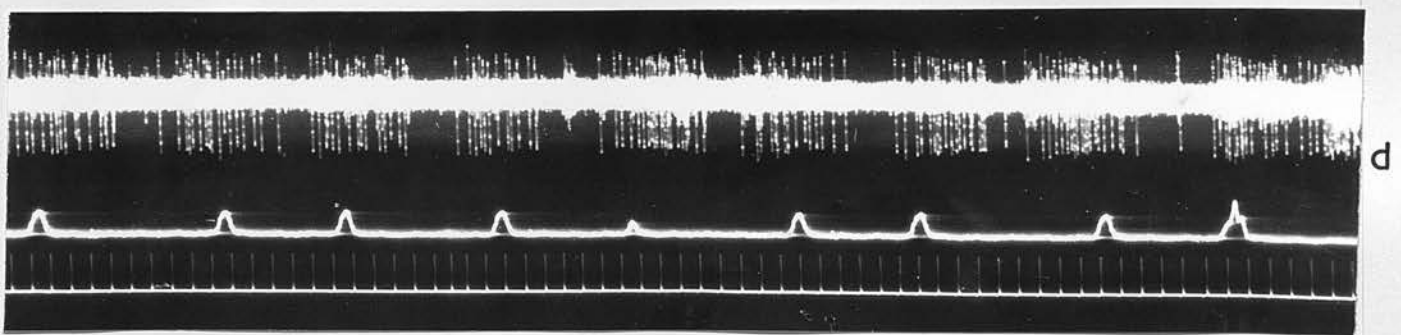
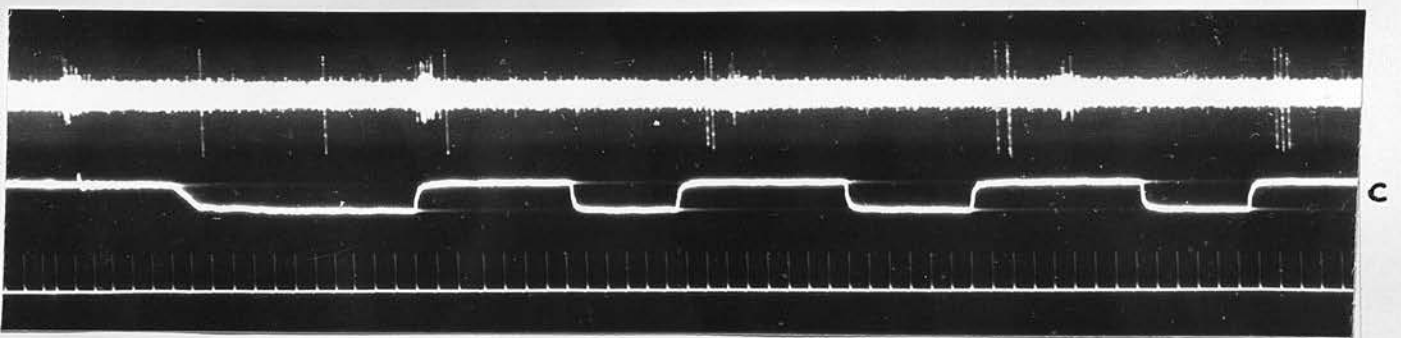
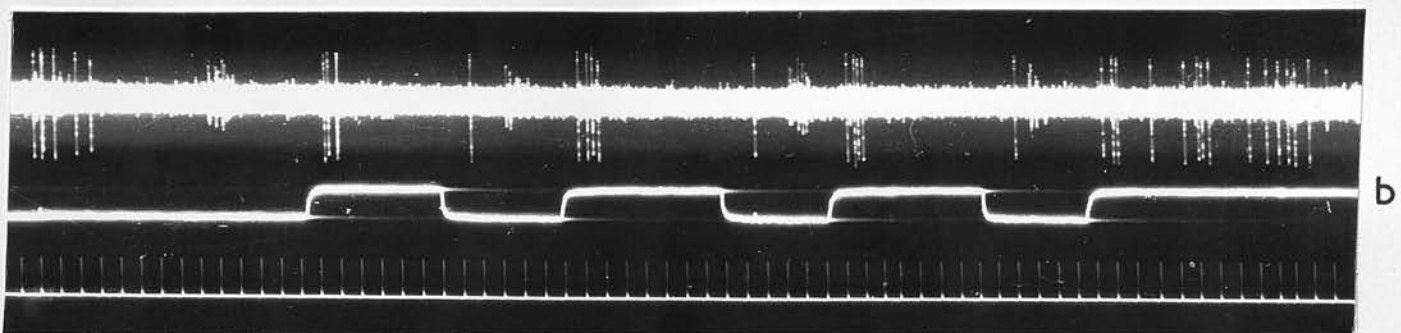
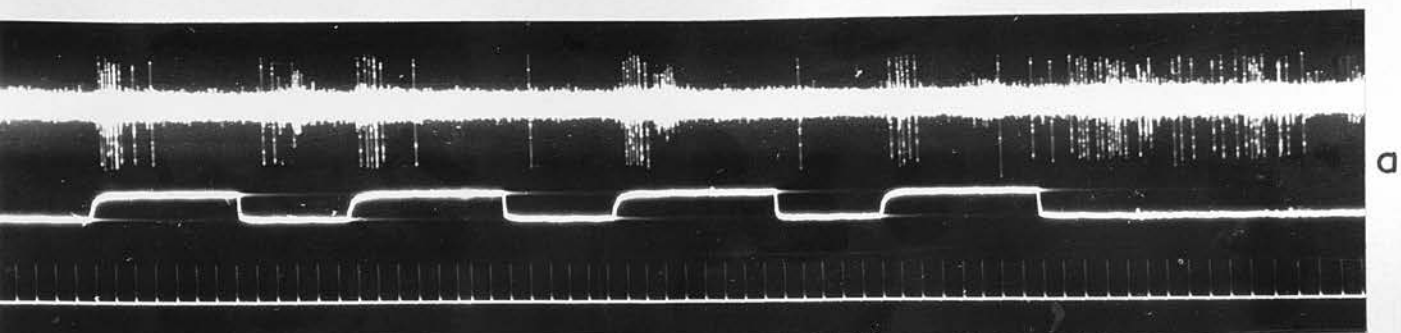
Conditions as above. 5° spot flashed 10° below the middle of the band region of the receptive field. Monitor trace upward movement indicates off of the light spot .

5° spot flashed 20° below the band region of the field .
Monitor trace as above .

5° spot flashed 30° below the band region of the field.
Monitor trace as above .

Vigorous firing is elicited from a long field unit when a 5° black disc is moved along the band region of the receptive field . Photocell output on monitor trace indicates entry and exit of the stimulus from the receptive field . The firing is , however , somewhat out of phase relative to the photocell output.

When the 5° black disc is moved along parallel to the band but 20° below its centre then the response is almost absent . The surround region then does not respond well to moving stimuli. Monitor trace as above .

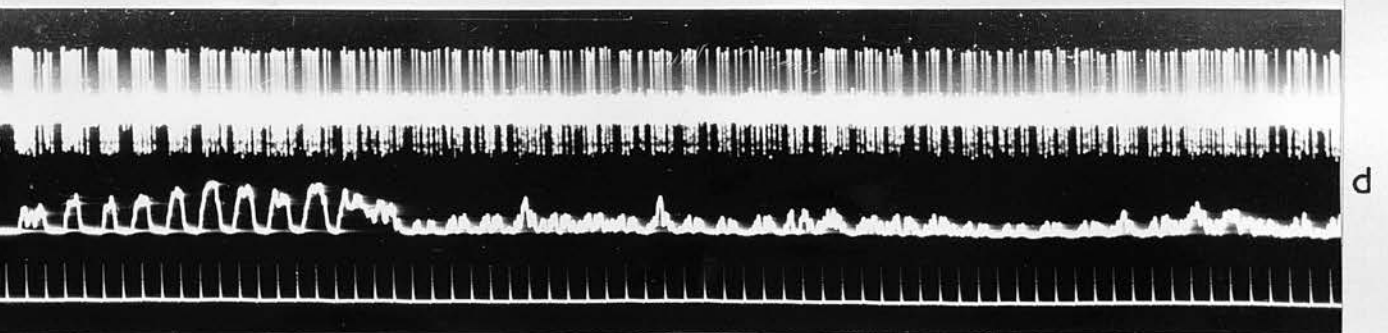
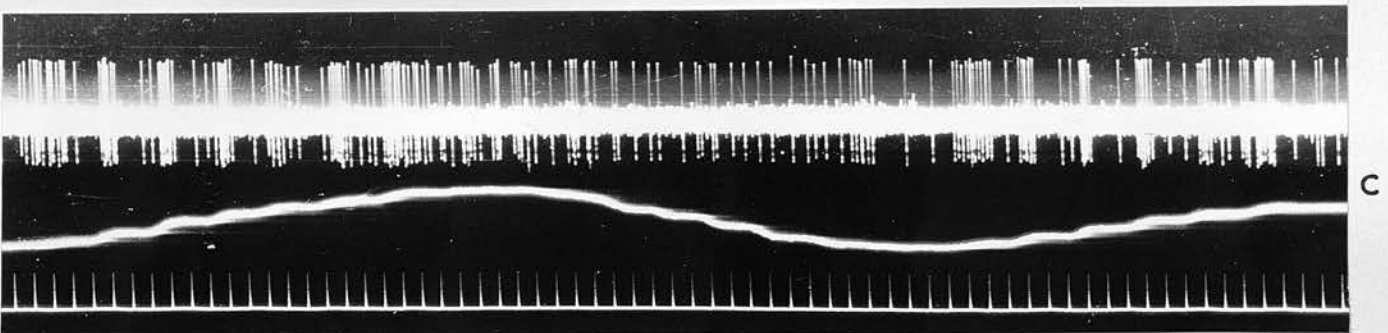
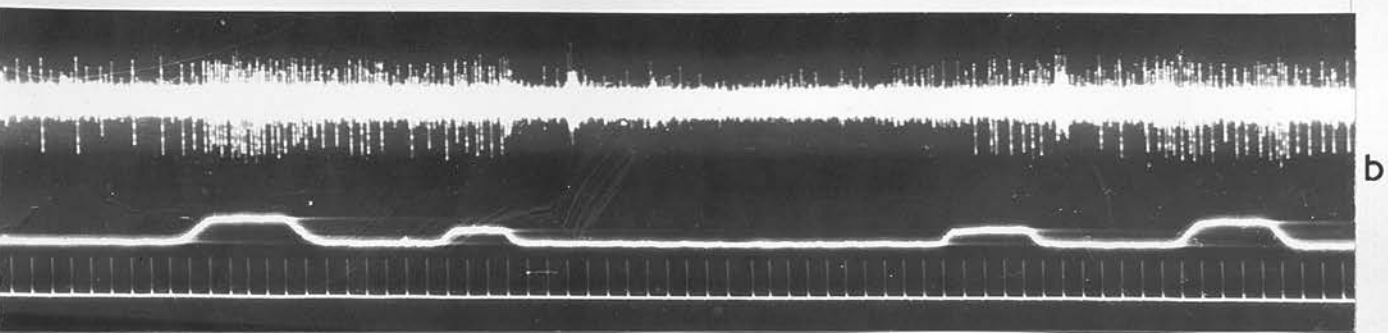
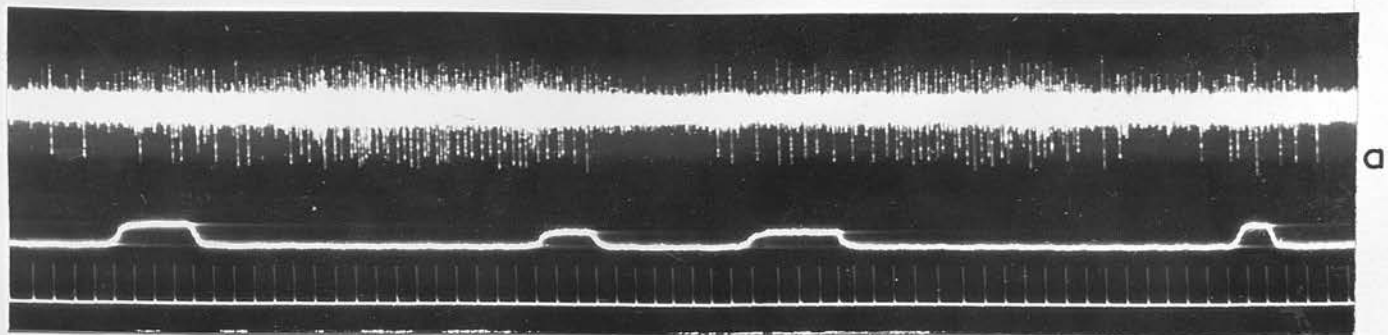


Response of a long field unit of the superior colliculus to the movement of a 5° card disc , black on a white background , along the band region of the receptive field. Bumps on the monitor trace indicate entry and exit of the stimulus in relation to the receptive field as recorded by phtocells placed one on each margin .

The conditions are here similar to those above excepting that the stimulus is moving across rather than along the band. The firing is equally powerful although naturally of shorter duration than above with constant velocity stimuli.

Response of a long field unit to step changes in light intensity. Dimming of the light is indicated by an upward movement of the monitor trace . Note the burst firing to decrements of light intensity and inhibition of the unit's maintained firing during increments in light intensity. The illuminated field is 5° in diameter .

Maintained firing of the long field unit readily falls into synchrony with the rapid movement of objects in the receptive field . The monitor trace moves up as the stimulus passes across the receptive field .



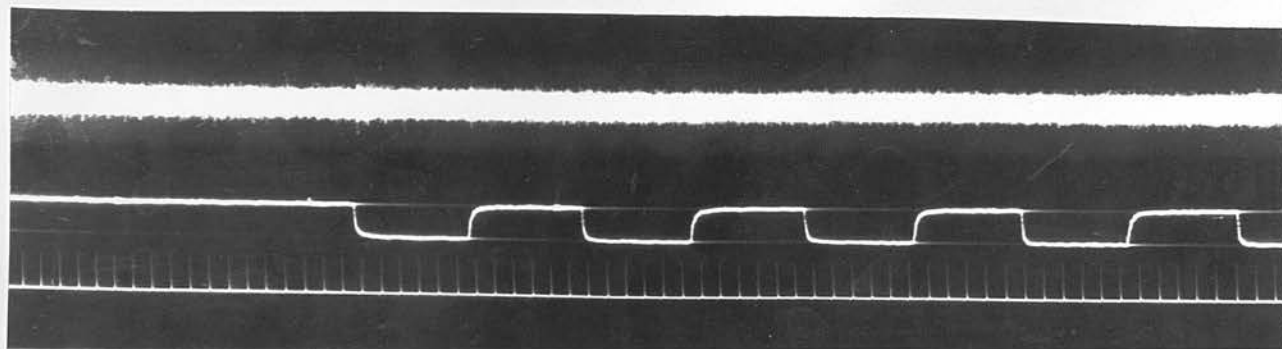
A characteristic unit lying 2.0 mm deep in the superior colliculus does not respond to flashing of a light spot on its receptive field.

Will not respond to whole field illumination .

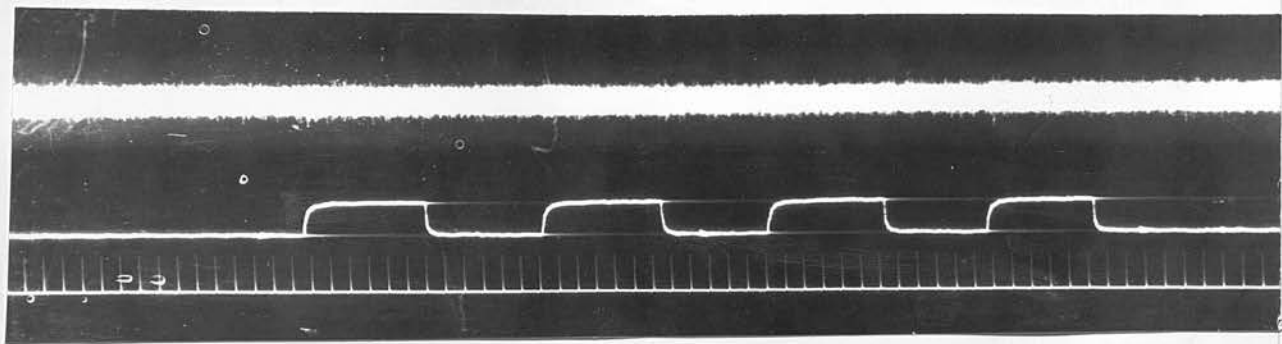
Will not respond to dimming or brightening stimuli.

Movement of a 2° light spot at $10^{\circ}/\text{sec}$. through the receptive field elicits a response . The upward movement of the monitor trace indicates the movement of the stimulus . The bumps on the trace indicate the passage of the stimulus over photocells mounted on each side of the receptive field .

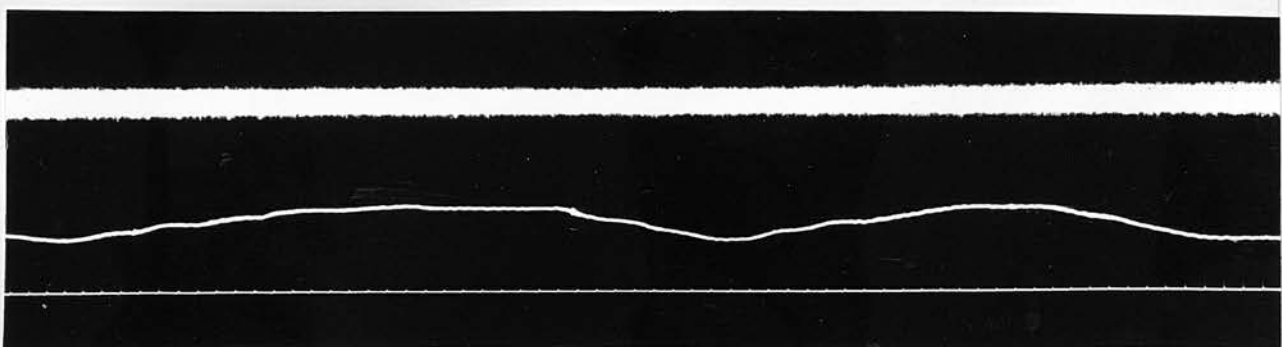
The unit habituates to the repeated presentation of the same stimulus which is in this case the passage of a 5° diameter black card disc through the receptive field. The photocell output which monitors the passage of the stimulus into and out of the receptive field is displayed on the monitor trace. The response ceases after three presentations .



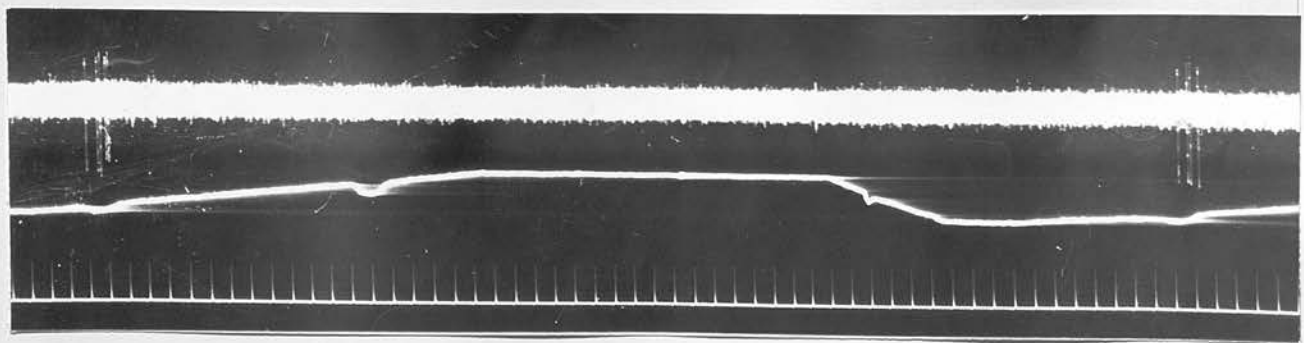
a



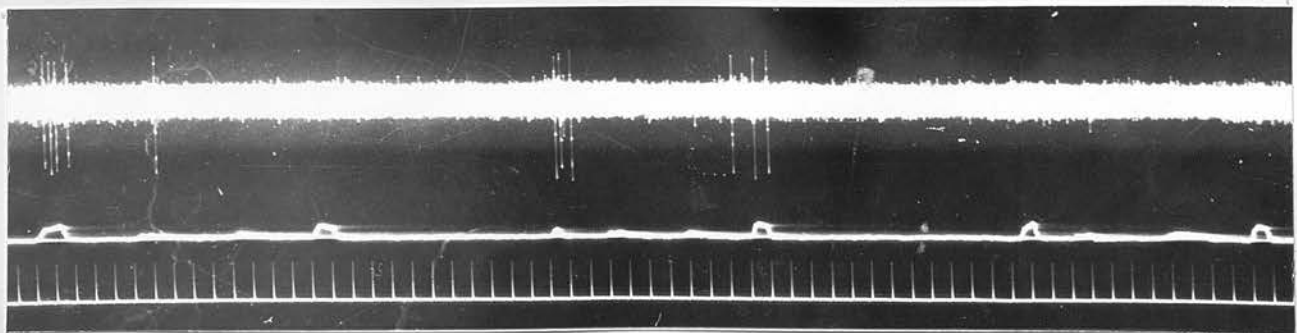
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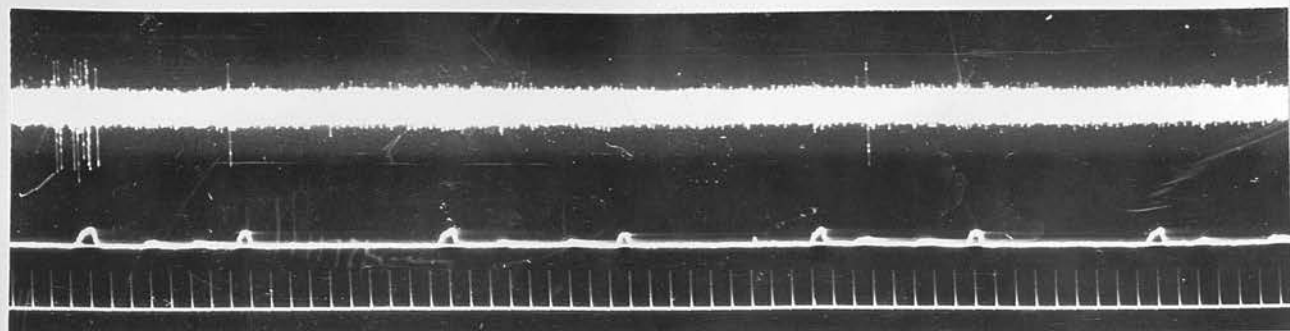


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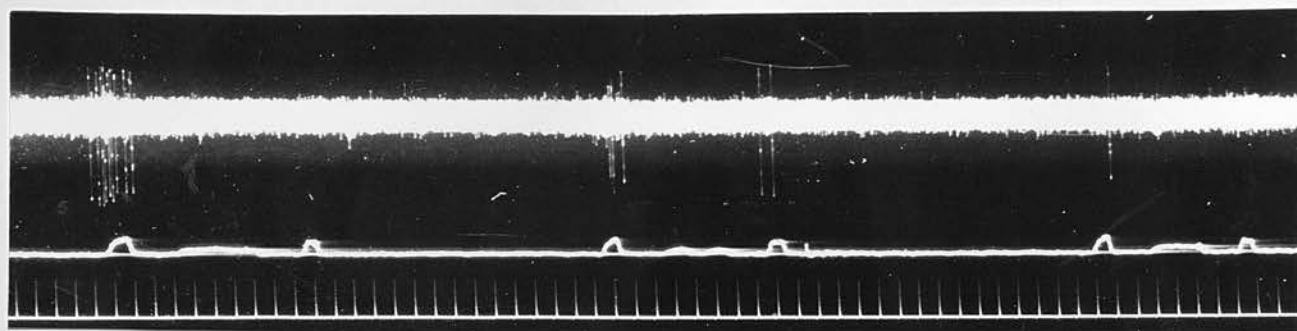
In this and the subsequent records the deep collicular unit has been habituated by repeated presentation of the same 50 black disc stimulus until firing has stopped . A 15 sec recovery period was then allowed and the stimulus once again presented . Habituation occurred in one presentation .

Same conditions as above but 30 sec. recovery period was allowed . Habituation occurs within two presentations except for one spike in the third presentation .

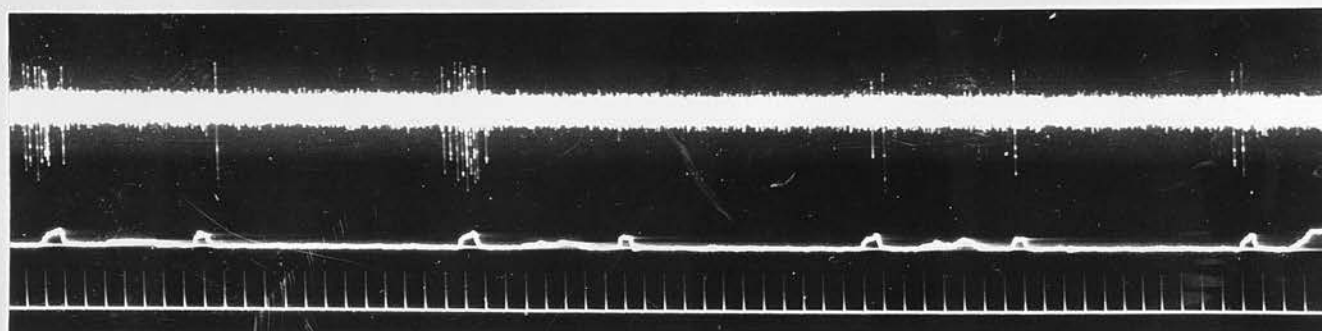
After 60 sec. recovery the unit requires more than four presentations for habituation to be re-established . Monitor trace indicates as above .



a



b



c

Hemifield unit recorded 2.5 mm below the surface of the superior colliculus. The unit is firing in response to the movement of a 10° card stimulus within its receptive field. The monitor trace indicates the output of a photocell as the stimulus passes over it in the receptive field.

A 2° black disc generates much more powerful firing.

The flashing of a 5° light spot elicits no more than one spike. Up of the monitor trace indicates on of the light.

Rapid movement of a black card stimulus into the receptive field elicits little response. The photocells are placed on each side of the receptive field region under investigation. The outputs sum when the stimulus covers both cells at once to give a double amplitude pulse. The movement is in the order of $300^{\circ}/\text{sec}$ in velocity.

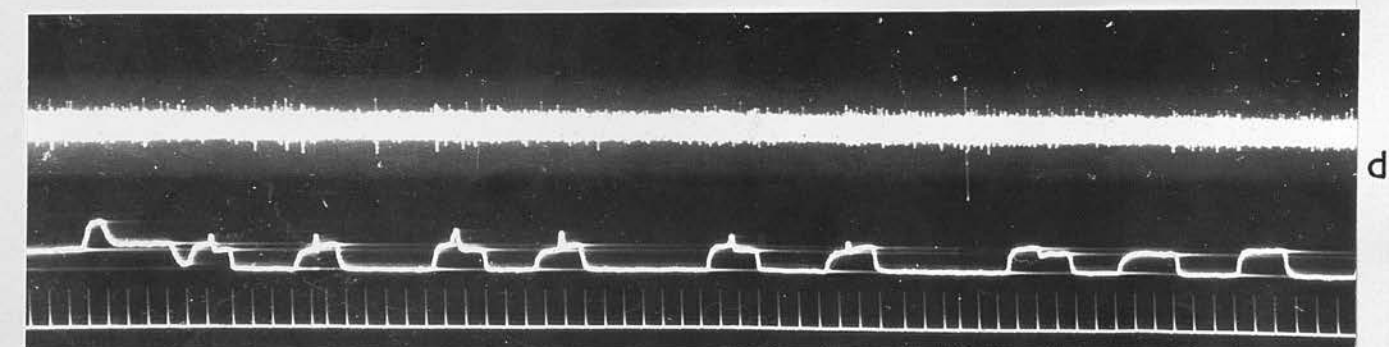
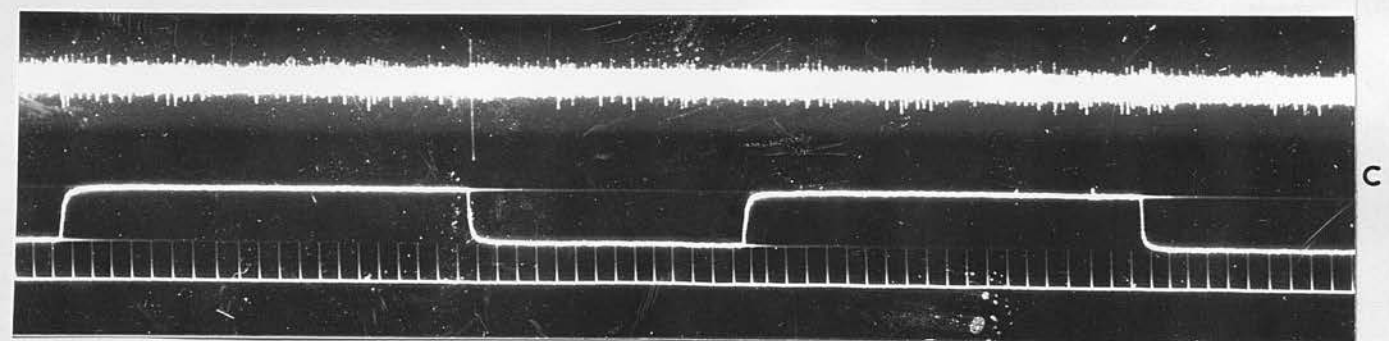
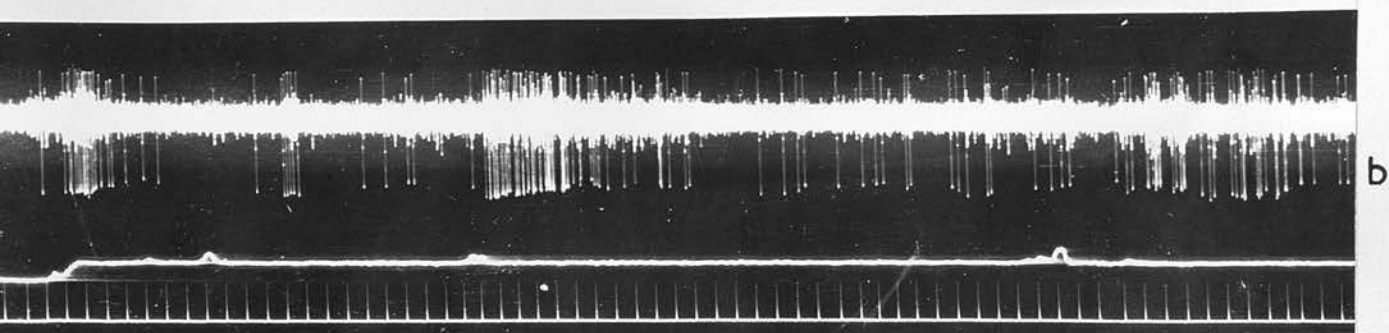
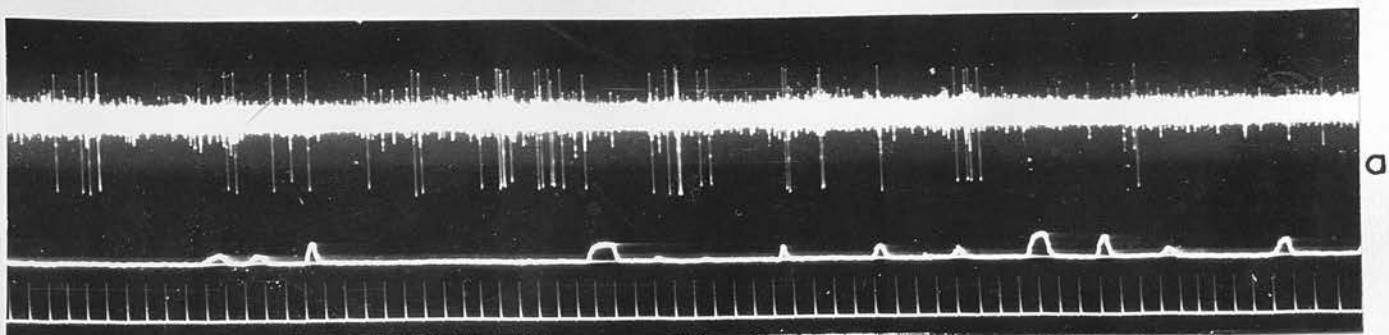
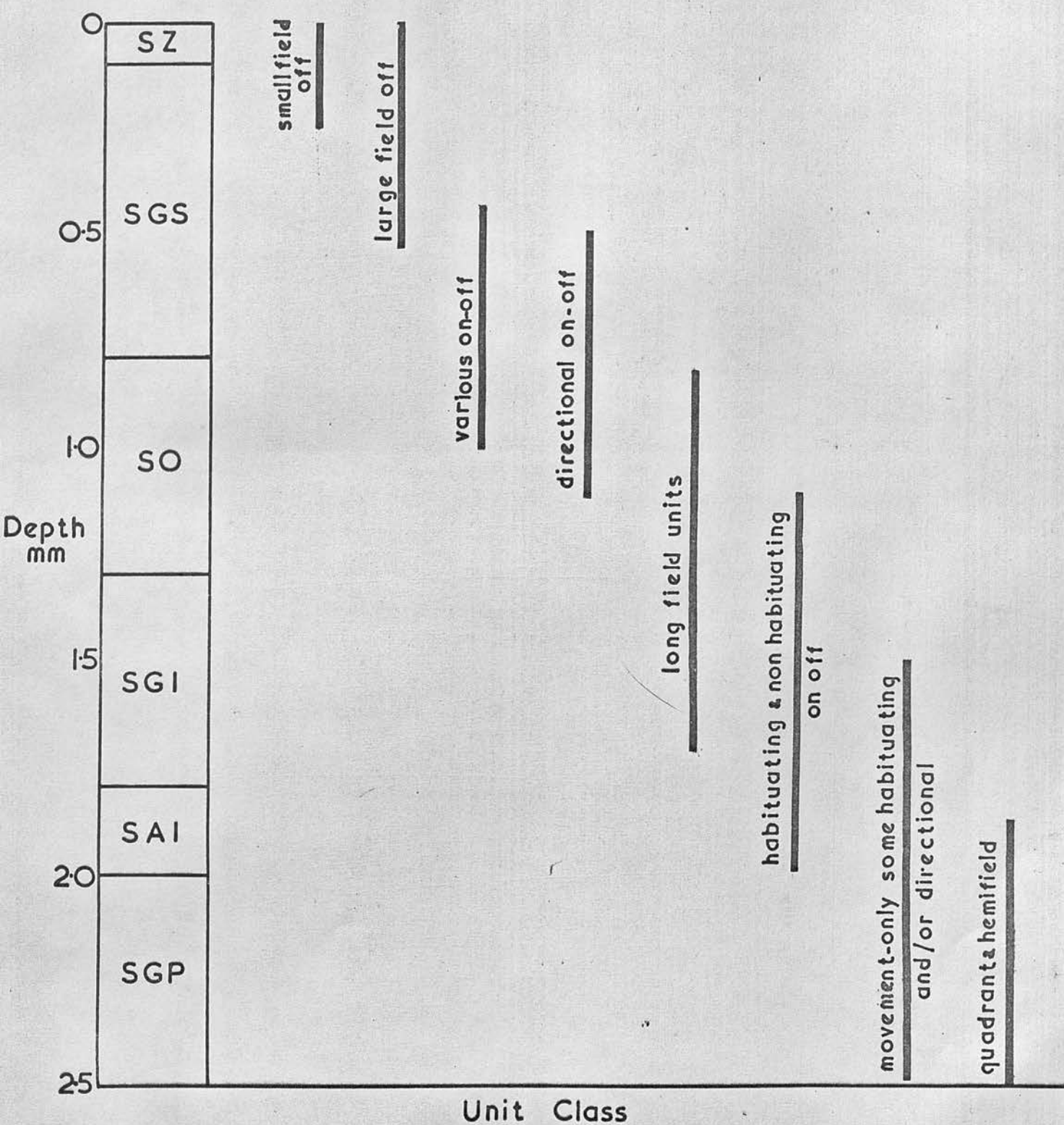


Fig.68. Lamination of unit classes in the superior colliculus. The ends of the black bars indicate the depth of the most superficial and of the deepest unit of each class encountered in the superior colliculus. An approximate scale indicates the laminae of the superior colliculus in relation to the depth measurements.



CORTICO-TECTAL PATHWAY

INTRODUCTION

A pathway from the striate cortex to the superior colliculus was demonstrated in the cat by Monakow (1889) and in the monkey by Ferrier and Turner (1890). These results have often been confirmed but the layers to which the cortical projection is made have not been clearly outlined. A detailed account of the pathway in the rat has been given by Lund (1966). Lesions made in area 17 (Lashley, 1941) of the rat gave rise to degenerating fibres which could be traced to the tectum. A few fibres pass to the stratum zonale but the majority pass to the stratum opticum or deep stratum griseum superficiale. A comparison of the positions of the cortical lesions made by Lund and the maps of rat cortex and colliculus determined by Forrester & La1(indicates that the strio-tectal projection of the visual field overlaps the direct retino-tectal map. Cortical lesions extending to layers III and IV alone did not produce collicular degeneration. It appears most likely that the fibres originate from the large pyramids of layer V. A second cortical projection was shown to exist from the regions anterior and medial to the striate area. The fibres do not terminate in regions above the stratum griseum intermediale.

Little evidence exists for the occipitotectal path in the rabbit. Monakow's finding (1881) that lesions to the striate cortex of new born rabbits produced degenerative changes in the superior colliculus was not confirmed by Putnam and Putnam (1926). Both Cajal (1911) and Leblanc (1928) describe, however, an occipitotectal path in the rabbit. According to the results of Gerebtzoff and Wauters (1941), the projection is not topographically organised but the data is limited. Since this work was completed, Giolli et al. (1967) have published a description of the topography of the projection of both Visual I and Visual II on to the superior colliculus of the rabbit,

In view of the evidence mentioned previously for a direct cortico-collicular projection in the rabbit it was thought of interest to determine the nature of the adequate stimulus of those units receiving the cortical projection. Another worker in this laboratory (Vejbaesya, 1967) has recently demonstrated /

demonstrated that cooling of the cat visual cortex causes the loss of visual response in certain directional and orientation sensitive units of the superior colliculus. The spontaneous activity of the units remain and after the cessation of cooling the response to visual stimuli returns in a short time. A number of attempts to apply this technique to the rabbit failed.

In a few crude experiments the whole upper occipital cortex was removed by suction from one hemisphere thus leaving the lower cortex intact and acting as a protective cover for the colliculus. No marked difference between the events occurring during a stab into these or normal colliculi was noted. Spontaneous activity between about 1.0 mm. and 3.0 mm. was more marked than usual but the usual types of visually responsive units were recorded. The visually responsive units did not, however, show much spontaneous activity. These findings are similar to those in the rat (Humphrey, personal communication).

It was thus decided that an attempt would be made to demonstrate the cortico-tectal path by means of strychnine neuronography.

METHODS

The animal was prepared in the usual fashion under urethane anaesthesia but paraffin instead of agar was applied to the cortex. Maps of the projection of the visual field on to the cortex and colliculus of the right side were made with a tungsten electrode. A region of cortex to which the nasal visual field projected was chosen to receive the strychnine for it was well removed from the region of brain which had to be penetrated by the microelectrode in order to reach the corresponding region of the superior colliculus projection.

Strychnine was applied to the cortex by means of 1 mm. squares of filter paper soaked in 1% strychnine nitrate solution which were placed on the chosen region. A small cotton wick electrode contacted the adjacent cortex and indicated the occurrence of strychnine spikes. A microelectrode was used to record activity in the corresponding region of the superior colliculus /

colliculus. The technique is that introduced by Dusser de Barenne and McCulloch (1938).

RESULTS

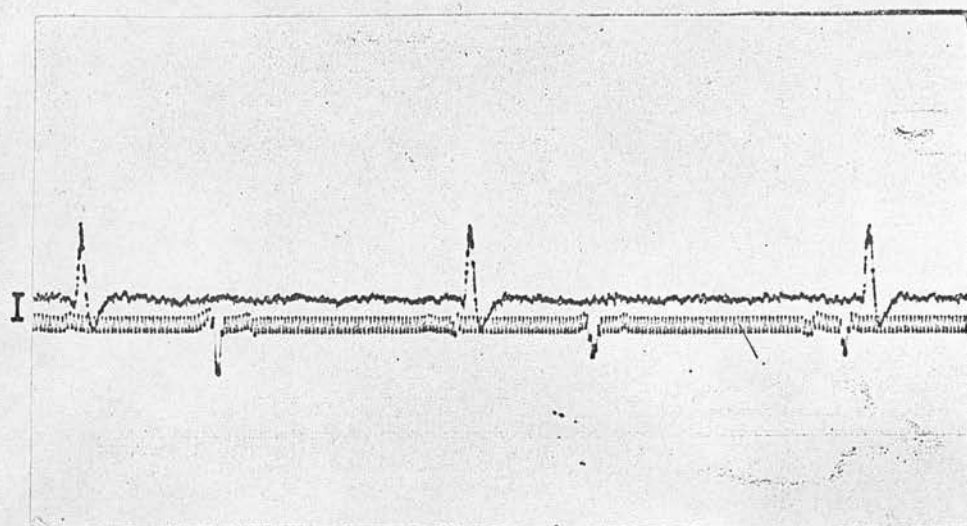
After about 5 minutes of strychnine application the cotton wick monitor electrode revealed the development of strychnine spikes (fig. 69). When the electrode was about 0.5 mm. down in the colliculus it was possible to hear a faint hiss which occurred synchronously with the cortical strychnine spikes. At a depth of 1 mm. the bursts were pronounced and it was possible to record small amplitude single units firing in synchrony with the cortical bursts. Between 1 and 2 mm. down a number of long field units were recorded which showed a small burst of firing followed by a short period of inhibition after each cortical spike (fig. 69). The properties of the units were apparently normal and their fields were readily mapped out. Spontaneous and burst activity was found up to a depth of about 3.0 mm. in two animals.

By the time these observations had been completed it was found that the cortical strychnine spikes had begun to spread out from the region to which strychnine had been applied. This may result from a combination of neural and diffusion phenomena. The spread prevented the demonstration of the topography of the cortico-collicular projection.

DISCUSSION

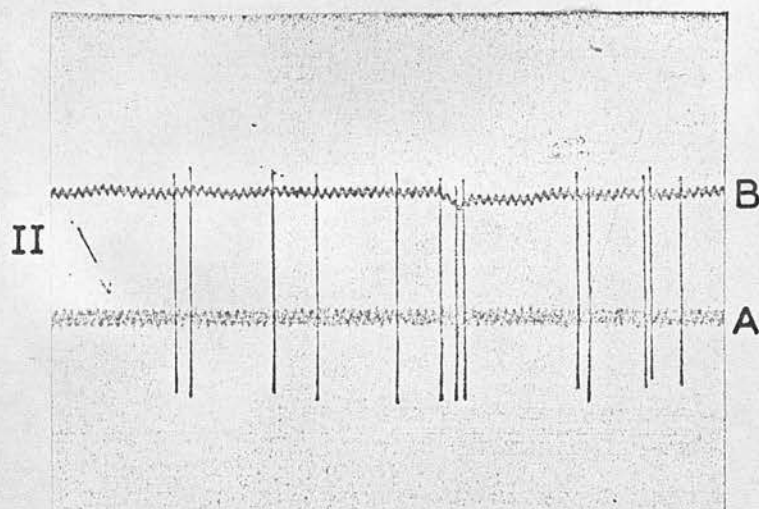
The appearance of burst firing in the superior colliculus at a time when the cortical strychnine spikes are localised to a small area suggests that a substantial fibre projection exists connecting the two regions. The collicular fibre bursts occur about 10 m.s. after the cortical spike. The cortico-tectal path described anatomically is about 15 mm. long which indicates fibres with a conduction velocity of about 1.5 m/sec. Lund (1966) comments that, in the rat, the cortico-tectal fibres appear to be, on the average, smaller than those of the retino-tectal path.

It is impossible to deduce the nature of the normal cortical influence on the cells of the superior colliculus from their response to the barrage of impulses arriving in the cortical efferents. The experiment gives physiological indication of no more than the presence of the cortice-collicular path and this confirms the findings of Giolli et al. (1967).



CORTICAL STRYCHNINE
SPIKES RECORDED BY

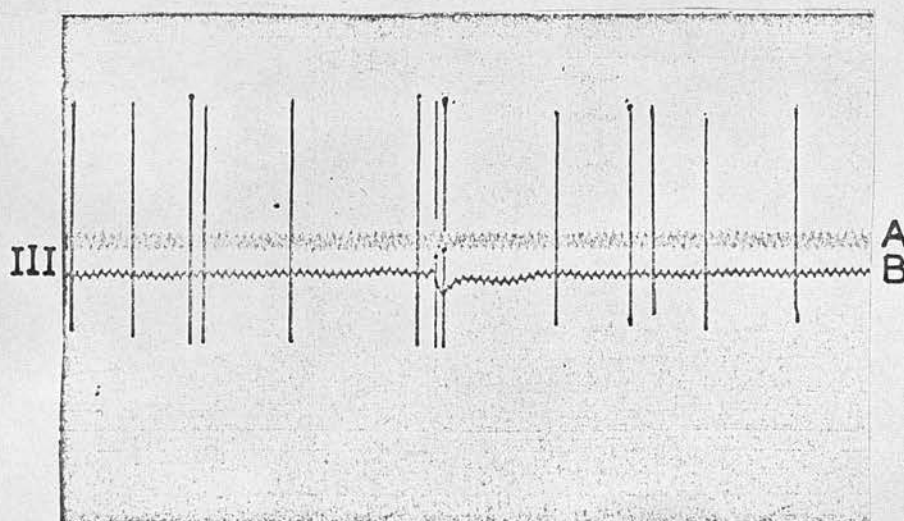
MICROELECTRODE (A)
COTTON WICK (B)



(A) BELOW SHOWS
MICROELECTRODE
RECORDING OF LONG
FIELD CELL ACTIVITY
1 MM DEEP

(B) SHOWS SIMULTANEOUS
WICK RECORDING OF
VISUAL CORTIX
STRYCHNINE SPIKES

BOTH ELECTRODES
AT N50°, 0°



THE LATERAL GENICULATE NUCLEUS

The rabbit lateral geniculate nucleus is generally recognised as consisting of two parts, the pars dorsalis (DLGN) and the pars ventralis (VLGN). The termination of the optic tract fibres in these two regions has already been discussed along with information which suggests that the dorsal nucleus of the rabbit LGN may, in contrast to the usually accepted view, be laminated in the area of binocular representation.

PARS DORSALIS

The extent to which the LGN pars dorsalis is subdivided varies from author to author. Winkler and Potter (1911) and Sawyer, Everret and Green (1954) do not indicate any subdivisions in their maps. Rose (1935), however, describes dorso-oral α , dorso-caudal γ , ventro-oral β and ventro-caudal components. Rose and Malis (1964) recognise two components only; a large, somewhat crescent shaped, α region which contains, within its anterior hollow, a smaller more fibrous β portion. It appears likely that the β portions of Rose and Rose and Malis correspond.

Afferent Paths. The dorsal LGN is usually thought of as an independent relay nucleus which receives no input other than the optic tract axons. Contra-indications ~~however~~ exist. There is a considerable amount of electrophysiological evidence for an input from the reticular formation to the DLGN. The most convincing demonstration of this path has been made by Arden and Söderburg (1961), in the rabbit, whose experiments exclude the possibility of an indirect effect of the reticular formation on the DLGN via a centrifugal path to the retina. Scheibel and Scheibel (1958) demonstrated reticular formation neurons whose axons terminated in the DLGN in Golgi preparations of mouse thalamus. Cajal (1911) has described a path running from the midbrain up to the DLGN. The results of Hernandez-Peon (1956) suggest the presence of such a path in the cat.

No efferent tectal fibres appear to terminate in the DLGN of either rabbit (Tarlov and Moore, 1966; Cragg, 1962) or cat (Altman, 1961).

Evidence for a cortico-geniculate pathway has been available for some time /

time but until recently there has been little interest in its organisation. Cajal and Tello (1904) described fibres running from the internal capsule to the dorsal LGN where they ended in branching terminals. By the use of strychnine neuronography, Neimer and Jimenez-Castellanos (1950) demonstrated a projection from area 17 to the DLGN in the cat. According to Widen and Ajmone Marsan (1960) and Szentagothai (1966) the corticofugal fibres to the LGN originate in the parastriate and prestriate regions of the cat. Altman (1961) describes only a sparse projection from the striate area of the cat to the DLGN. Garey (1965) and Guillery (1967) claim striate projections to the LGN, while Kusoma (1966) describes Visual I alone as projecting to the LGN. A path from areas 17 and 18 to the dorsal LGN has been described in the rat by Nauta and Bucher (1954). The results of Leblanc (1928), Biernond (1930) and Cragg (1962) indicate that this path is present in the rabbit.

Efferent Paths. The main efferent projection of the DLGN is to the striate cortex. The outline of the cortical areas receiving this projection was first demonstrated in the rabbit by von Monakow (1881) using retrograde degeneration. The detailed topography of the connections was elucidated in more detail by Putnam and Putnam (1926) and later by Rose and Malis (1965).

The results of Polyak (1933) and Lashley's (1934) work on monkey and rat suggested that all LGN cells showed retrograde degeneration after striate cortex removal. Minkowski's results on the cat did not support this view (1913). Fischman and Meikle (1965) and Wilson (1966) describe a population of small cells remaining intact after section of the cat thalamus medial and caudal to the LGN and removal of the visual cortex. The cells correspond in size with the short axon interneurons of O'Leary (1940). The electrophysiological results of Burke and Sefton (1966) indicate the presence of such interneurons in the rat so that Lashley's findings are certainly wrong. Many of the cells remaining after simple striate ablation will be those giving rise to the other geniculate efferent paths.

A considerable literature exists on the LGN projections to cortical regions outside area 17 in the cat. Wilson and Cragg (1967) have recently published a useful description of the connections which is based upon their own work. The cat LGN was found to give rise to four cortical projections. Two of these possessed a similar topography in the LGN, one projecting to area 17 and the other to area 18. A third projection was found to the suprasylvian gyrus. The most medial patch of cells in the dorsal nucleus of the LGN, which was designated the medial interlaminar nucleus by Thuma (1928), was found to give rise to an independent projection to area 19. This nucleus was shown to receive a projection from the retina by Stone and Hanson (1966). These results were confirmed by Garey and Powell (1967) who, in addition, demonstrated that the small geniculate cells give rise to projections to area 17 while large cells project to areas 17 and 18.

Anatomical evidence for such multiple projections is lacking in the rabbit although von Monakow (1882) did suggest that pathways to regions outside the visual cortex arise from the LGN of that animal.

Altman (1962) and Cragg (1962) show results suggestive of a geniculotectal path in the cat and rabbit respectively but damage to optic tract fibres may have occurred when the LGN lesions were made. Gudden (1886) has, however, also described such a path in the rabbit.

A number of other projections from the cat LGN were also described by Altman (1962) amongst which are paths to the ventral nucleus of the LGN, pretectum, pulvinar and nucleus lateralis posterior. The connections of these regions are not clear in the cat while no similar investigations have been carried out on the rabbit.

PARS VENTRALIS

The rabbit ventral nucleus of the LGN is subdivided by Winkler and Potter (1941) into two components, a lateral 'a' portion containing many fibres and a more medial 'b' portion possessing a dense population of small cells. Rose (1931) describes α , β and γ regions of the nucleus.

Afferent /

Afferent Paths. It appears fairly certain that the pars ventralis of the rabbit LGN receives optic tract fibres (page 73).

Cragg (1962) and Tarlov and Moore (1966) describe a discrete projection from the superior colliculus, through the brachium quadrigeminum, to the VLGN in the rabbit. The path has been observed in the cat by Altman and Carpenter (1961).

Fibres have been observed passing from the DLGN to the ventral nucleus in the cat (Altman, 1962).

The ventral nucleus has been observed to receive fibres from the striate cortex in a number of animals. Such a path is described by Altman (1962) and Nauta (c.f. Wijen and Ajmone Marsan, 1960) in the cat, by Nauta and Bucher (1954) in the rat and by Cragg (1962) and Leblanc (1928) in the rabbit.

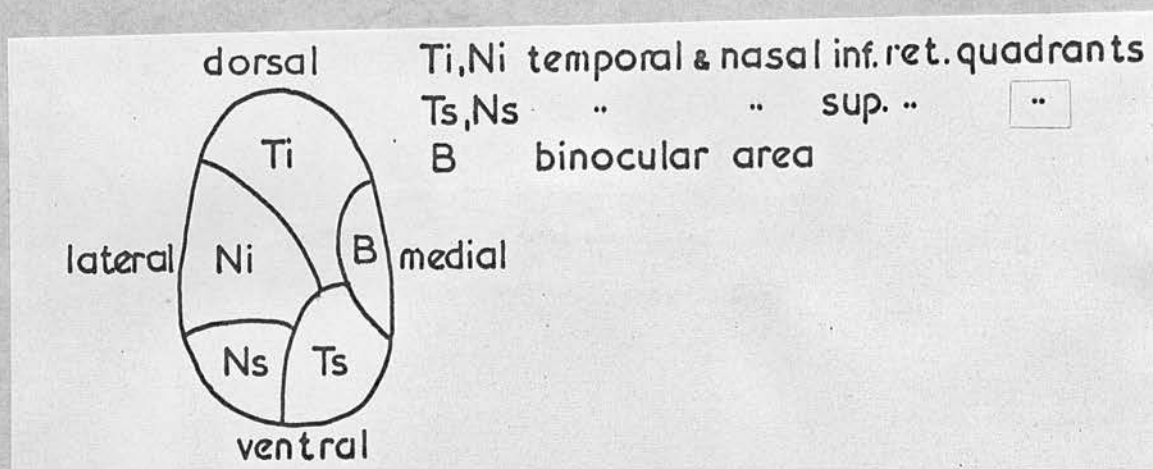
Efferent Paths. Very little is known about the efferent connections of this nucleus. Altman (1962) has found indications of paths to the centrum medianum, thalamic reticular nucleus and the subthalamus. No retrograde degeneration of the ventral nucleus has been observed in either cats (Waller and Barris, 1937) or rabbits (Rose and Malis, 1964) after removal of the striate cortex.

The great variety of reported connections suggest that the ventral nucleus of the LGN may play an important role in the visual mechanisms of the lower mammals. Confirmation of the above reports should be effected.

TOPOGRAPHY OF THE RETINO-GENICULATE PROJECTION

INTRODUCTION

The first mapping of the projection of the retinal quadrants on to the lateral geniculate nucleus was carried out by Brouwer et al. (1923) who made limited retinal lesions and traced the subsequent degeneration in the CNS by means of the Marchi technique. The projection of the visual field on to the dorsal nucleus was found to have the following appearance -



This map is not quite in agreement with that which was obtained electrophysiologically by Choudhury and Whitteridge (1965) but the error is not great. The topography of the connections between the DLGN and the visual cortex was determined by Rose and Malis (1964) by tracing retrograde degeneration subsequent to limited cortical lesions. Comparison of their map with the electrophysiologically determined projection of the visual field on to the visual cortex confirms, in substance, the findings of Choudhury and Whitteridge.

It was not possible to replot the data of Choudhury et al. (1965) or Choudhury (1964) to conform accurately with the standard eye position and coordinate system used here because the eye orientation and optic nerve head projection are not given in the protocol.

Choudhury et al. describe the presence of a second representation of the visual field in the medio-caudal region of the dorsal nucleus but the available /

available data does not enable a coherent set of coordinate lines to be drawn through the area.

According to Brouwer et al. (1923), the dorsal surface of the LGN receives the projection of the nasal and some of the temporal upper field on its medial and lateral edges respectively. The results of Rose and Malis (1964) do not suggest that this arrangement should alter in passing along the antero-posterior axis of the nucleus. Choudhury et al. (1964), however, show a projection map of the dorsal surface of the LGN in which the visual field is represented from the + 30° parallel at the anterior end to the - 40° parallel at the posterior end of the nucleus. An examination of their transverse maps of the LGN reveals, however, that the most posterior section possesses a representation of the region above the horizontal and that the field below the horizontal should not be represented in the dorsal projection of the nucleus.

Experiments were thus undertaken for the purpose of investigating the second representation of the visual field, the projection of the visual field on the dorsal surface and the volumes occupied by the projection of the various regions of the visual field in the LGN when the eye is in the standard position.

METHODS

The animals were all investigated under urethane anaesthesia. The LGN was reached by tungsten electrodes inserted through the cortex and aimed stereotactically. In Sawyer et al.'s coordinate system (1954) the LGN lies from 3 to 6 mm. behind Bregma and about 5 to 8 mm. lateral of the midline. The procedures used in preparation and mapping were similar to those described in the main methods section and differed from those used in exploring cortex and superior colliculus only in that several mapping points were obtained during each stab. Readings were made at 300 μ intervals during a stab while subsequent electrode stabs were made in a matrix with 0.5 mm. intervals. Histological verification of the presence of the electrodes in the LGN during recording /

recording was made subsequently by the usual methods.

RESULTS

The data required for the construction of an extensive and detailed map of the DLGN takes a considerable length of time to collect because, unlike the case of the colliculus or cortex, it is necessary to form a three dimensional matrix of examined points within the brain. Several incomplete maps were constructed but, out of 7 attempts, two almost complete maps were obtained. The best of these is shown in figures 70-77 and is based upon some 250 points recorded in nearly 50 stabs. The experiment took more than 30 hours to complete.

Figure 70 represents the extent of the visual field which is histologically confirmed to be projected on the surface of the lateral geniculate dorsal nucleus. Only the vertical meridia are marked in. It may be seen that the temporal field receives a lesser representation than the nasal in this aspect. The parallels have not been marked in because the points recorded are rather too irregular for satisfactory lines to be drawn. Examination of the recorded altitudes indicates, however, a tendency for points at the anterior end of the LGN dorsal surface to represent regions of greater altitude than those of the posterior end. The greatly compressed representation of the parallels above about 15° conspires to introduce considerable inaccuracy into this form of map because the electrode is advanced in steps of about 300 μ until a response has been identified as coming from the LGN and thus, in some areas, as much as 25-30° of visual field representation may be lost in the initial step.

In the posteromedial part of the surface is a region containing a second mirror image representation of the more nasal part of the visual field. This map is on a reduced scale and not many points are recorded from the tissue containing it.

The diagrams of figs. 71 - 76 illustrate the projection of the visual field on to coronal sections through the LGN. The series of diagrams runs anterior to posterior by steps of the magnitude shown. Subsequent to /

to the experiment, the coronal sections most closely corresponding to the plane of each mediolateral row of electrode stabs were identified. The slides were photographed at a suitable magnification and the electrode tracks were marked in. The visual field coordinates represented at each examined point on the track were indicated after which the meridians and parallels were drawn on a transparent overlay.

The maps of the projection of the visual field on to the transverse sections through the DLGN show the temporal visual field to be represented laterally in the nucleus and the nasal field medially. The upper field is represented dorsally and the lower field ventrally.

It is immediately apparent that the visual streak, i.e. the region of field from 10° to -10° (page 163), receives a disproportionately large representation in all of the LGN transverse sections. In all cases the nasal field representation occupies a greater area than that of the temporal field. The expansion of the nasal representation is confined to the most anterior 40° . The field is represented for about 75° nasal and temporal of the meridian coinciding with the projection of the optic nerve head. The lower field is represented down to about the 50° parallel. The most anterior coronal section of the LGN appeared to contain a representation of the upper field as far as the 80° parallel but at the posterior end of the nucleus the 10° parallel is the highest to appear.

Binocular responses were obtained in a region which extended caudally along the medial edge of the nucleus for at least 0.5 mm. from a plane lying 1 mm. behind the anterior margin of the LGN. The responses were recorded throughout the whole depth of the nucleus in the case of the stabs on the medial margin.

The coronal sections through the LGN clearly show the presence of a second representation of the visual field which lies along the medial edge of the nucleus and in mirror image relationship to the primary projection. Not many points were recorded from this region but meridians and parallels consistent with those of the primary projection could usually be drawn through them /

them. The second map of the visual field contains regions of the field nasal of the N 20° meridian. In some cases a few points have been obtained from regions representing the central part of the temporal visual field. The representation appears to be confined to the DLGN but may extend a little beyond its apparent borders in some cases.

It is to be noted that a limited portion of the projection of the visual field on to the ventral nucleus of the LGN has been recorded in figure .

A single coronal section of the DLGN which was obtained in an unfinished experiment is displayed in fig. 78. The section is taken 1.28 mm. behind the anterior plane of the LGN and corresponds roughly to section 3 of fig. 73 from experiment (269). The map clearly shows both the binocular area and the second representation of the visual field.

The main features of the above maps are similar to those of maps obtained in other experiments. In two cases, however, the projection of the visual field on to the most anterior section through the LGN has been seen to contain a more extensive representation of the temporal than the nasal field. In one case the meridia appeared to be more widely spaced in the temporal visual field than in the nasal.

In other maps the most posterior section is quite commonly found to contain a representation of the nasal field alone.

Magnification Factors. Magnification factors along the equator of the visual field and along the vertical meridian whose projection passes through the optic nerve head have been measured on each of the coronal sections of figs. 71-76. The horizontal M factor results are shown in fig. 79A and the vertical in fig. 79B.

Visual Field Volume Representation in LGN. The visual field projection on to the LGN is not distributed along a flat sheet of uniform thickness, as is the case in the visual cortex or superior colliculus, so that estimation of the percentage of the tissue devoted to various parts of the projection within the nucleus is best carried out in terms of volumes.

The /

The projection of the visual field into the LGN was divided, by lines drawn along suitable meridia, into four components subtending equal angles along the parallels. These subdivisions were referred to as temporal posterior, temporal anterior, nasal posterior and nasal anterior. The 10° and the -10° parallels were chosen to represent the boundaries of the visual streak representation (page 163) and the visual field was subdivided into three components along the vertical, upper, streak and lower field.

The area of each coronal section devoted to the representation of each of these 12 regions was estimated by counting squares on graph paper viewed through a drawing of the map made on tracing paper. The projection lines of a map in any coronal section were assumed to be identical in all anterior and posterior planes up to those half way from the section considered to the next anterior or posterior coronal section. Each of the twelve areal subdivisions of the coronal sections is thus assumed to be of thickness equal to the sum of one half of the distance from the coronal plane considered to the next anterior and posterior sections. The volume of tissue representing a given region of the visual field within each slice of LGN may thus readily be computed by forming the product of the area of its projection and of the thickness of the slice. The total representation of that region of visual field is obtained as the sum of the appropriate volumes from each slice.

The computed volumes of LGN tissue devoted to the representation of each of the 12 subdivisions of the visual field are shown in Tables V/ and V//. Table V/ contains the results for the brain whose complete map is illustrated above. A second component of the table gives the volumes of each element of the representation as a percentage of the total LGN volume. The total at the foot of each column of the table expresses either the volume or percentage of the LGN which is devoted to the representation of each quarter of the represented visual field. The final section of each table shows the volume of each quarter of the visual streak representation as a percentage of the total streak representation.

DISCUSSION /

TABLE VI Volumes of LGN Tissue Devoted to the Representation
of Various Elements of the Visual Field Projection
(U, upper field; S, streak field; L, lower field)

RABBIT 1

Volumes of each element of visual field, in mm³

Temporal post. half	Temporal anter. half	Nasal post. half	Nasal anter. half	
0.61	0.52	0.52	0.53	U
1.14	1.44	1.44	1.88	S
0.52	0.57	0.46	0.72	L
2.24	2.53	2.41	3.13	Column Total
				<u>Total Volume 10.3 mm³</u>

Each element as % of total LGN volume

Temporal post. half	Temporal anter. half	Nasal post. half	Nasal anter. half	
6.0	5.0	5.0	5.0	U
11.0	14.0	14.0	18.0	S
5.0	5.5	4.5	7.0	L
22.0	24.5	23.5	30.0	Column Total

Elements of visual streak alone

1.14	1.44	1.44	1.88	mm ³
19	24	24	33	% of total streak
				<u>Total Volume 5.9 mm³</u>

Temporal Streak
% of LGN volume
25%

Nasal Streak
% of LGN volume
32%

Streak
% of LGN volume
57%

VII RABBIT 2

Volumes of each element of visual field, in mm³

Temporal post. half	Temporal anter. half	Nasal post. half	Nasal anter. half	
0.41	0.41	0.37	0.41	U
0.95	1.11	1.16	2.1	S
0.14	0.17	0.31	0.82	L
1.55	1.69	1.84	3.29	Column Total

Total Volume 8.37 mm³

Each element as % of total LGN volume

Temporal post. half	Temporal anter. half	Nasal post. half	Nasal anter. half	
5.0	5.0	4.3	5.0	U
11.3	13.0	14.0	25.0	S
1.7	2.0	3.7	10.0	L
18.0	20.0	22.0	40.0	Column Total

Elements of visual streak alone

0.95	1.11	1.16	2.1	mm ³
18.0	21.0	22.0	39.0	% of total streak

Total Volume 5.32 mm³

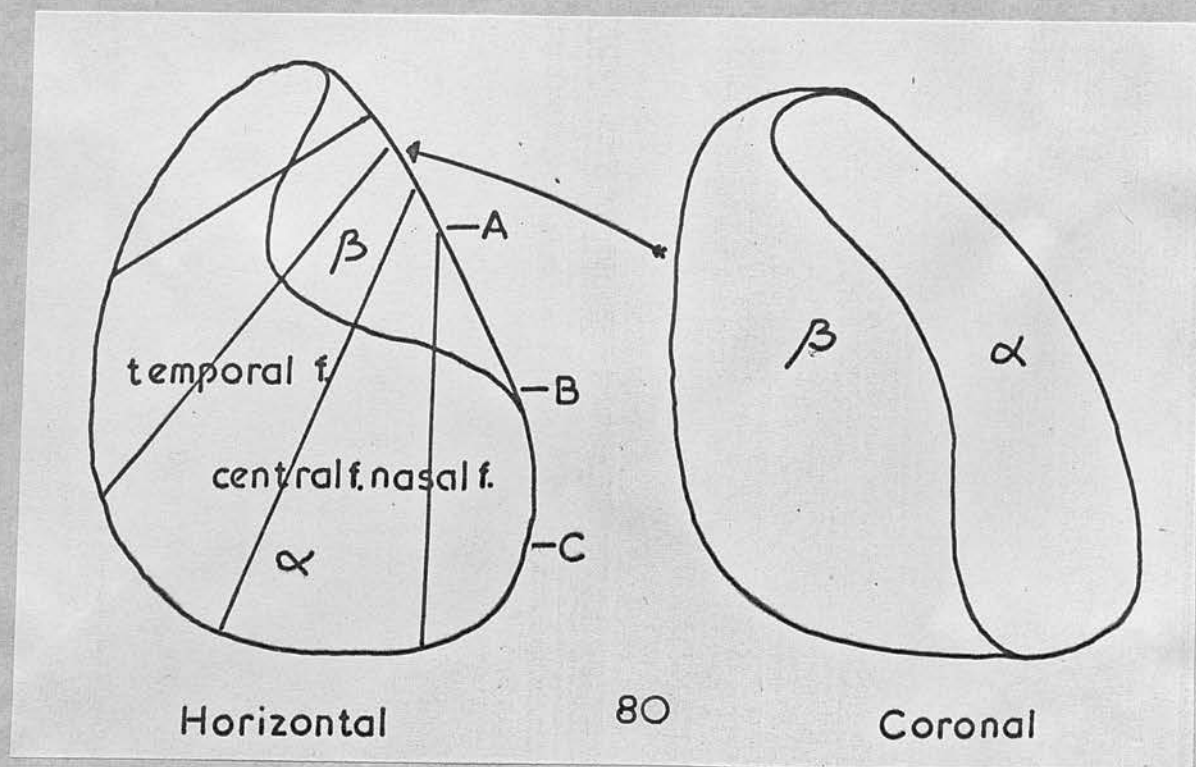
Temporal Streak
% of LGN volume
24%

Nasal Streak
% of LGN volume
39%

Streak
% of LGN volume
63%

DISCUSSION

LGN Structure and Visual Field Projection Topography. Rose and Malis (1964) describe the α or cellular portion of the LGN as being crescent shaped in horizontal section. The long axis of the cell ribbon runs orocaudally and then curves smoothly to continue in a lateromedial direction. It is claimed that the cells of the ribbon are arranged along radii which are perpendicular to the long axis of the ribbon. The position and size of the β sector is rather variable but fig. 80 below shows a common form. Each cell column appears to continue from the α into the β sector and projects on to a similar column of cells which runs radially through the visual cortex. The material of Rose and Malis did not reveal whether the β sector gave rise to projections different from those of the α region.



In the experiment on R1, which is described above, the first coronal section /

section passes through the plane containing the β sector. The visual field projection on to the section appears to be continuous through the α and β sectors. It would appear that the β region of the LGN may possess a lower proportion of cells than the α region but the arrangement of the maps does not suggest that the region receives a different projection to the α sector. The low cell density of the β region is probably a purely morphological feature resulting from the passage of the numerous efferent fibres from the α sector through its boundaries.

The coronal sections indicate that the anterior arm of the α sector, which extends above the β region, receives the projection of the extreme upper visual field (40° parallel and above) which does not receive a representation in the more posterior regions of the LGN. Rose and Malis found this region to project to the postero-medial visual cortex upon which extrapolation of present electrophysiologically determined projections of the visual field would suggest that the upper regions of the field are represented.

Close examination of the results of Rose and Malis reveals complete agreement between their description of the geniculo-cortical projection topography and the electrophysiologically determined projections described in this work.

The information provided by Rose and Malis suggests an explanation of the anomalous map forms sometimes encountered at the anterior and posterior limits of the LGN. Consider coronal sections made at A, B and C in fig. 80. At plane A the temporal field columns will pass at a shallow angle through the plane of section and thus the temporal M factors along the horizontal will be enhanced. On the other hand, the representation of the nasal field will receive a compressed representation in the medial sector. Such a situation corresponds to that in the map shown in fig. 81 which was the most anterior section of one experiment. The projection on to the plane intersected at B will contain a representation of most of the visual field and corresponds to maps such as are found in figs. 82. The most posterior /

posterior sections, such as C, will contain the representation of the nasal field alone. An example of such a map has been presented in fig. 93.

The map of the projection of the visual field on to the dorsal surface of the LGN shows that there is no representation of the visual field below the 10° parallel in this aspect. The results confirm the data of Choudhury and Whitteridge (1964) but not their map of the dorsal surface of the LGN.

Second Representation of the Visual field in the LGN. The results confirm Choudhury and Whitteridge's (1964) report of a second, mirror image, representation of the visual field along the medial edge of the nucleus in the more posterior sections. In spite of the relatively small number of points recorded from this region in each coronal section, it was possible to estimate the position of a few of the meridia and parallels; a feat not possible with the previously available data. The most medial point recorded, which represented part of the visual field on the T 20° meridian, lay just without the usually accepted boundaries of the LGN. No representation of the visual field beyond T 20° has been observed and the representation is more usually confined to the anterior part of the nasal field alone. It is possible that close examination would show the second representation of the field to extend into the regions adjacent to the LGN medial border but no evidence is available to suggest that this is the case. The region abutting the medial edge of the LGN has not been subjected to close anatomical examination in the rabbit and thus the map of Rose (1931), which shows extensive subdivision of other regions, neglects its description. According to Kuhlenbeck and Miller (1940) and Tarlov and Moore (1966), the posterior medial border of the DLGN is in close contact with the lateral edge of the posterior complex (continuation of the lateral posterior nucleus (Le Gros Clark, 1933)) along its upper part. The lower part of the border, where the visual field projection appears to extend a little beyond the LGN, abuts the rather diminutive pulvinar. Elucidation of the representation in this region will require separate investigation using small electrolytic lesions /

lesions as markers in order to obtain more precise localisation of the responses.

Seneviratne and Whitteridge (1962) and Bishop (196) have reported a second representation of the visual field on the medial aspect of the cat lateral geniculate nucleus. Vejbaesya (1967) has mapped this projection and shown it to lie in mirror image relationship to that in the main part of the LGN. He establishes the representation as lying in the medial inter-laminar nucleus. The position of this representation is similar to that of the second projection of the visual field in the rabbit LGN. It is natural to wonder if there is any similarity of function of the projection in the two animals.

The situation is, however, rather puzzling. It might be thought that the second representation is in the geniculate region which projects to the area occipitalis or visual II of the rabbit. The recent findings of Wilson and Gragg (1967) and Garey and Powell (1967) have shown that visual II, or area 18, of the cat receives its projection from the same portion of the LGN as visual I. The second field representation, or medial inter-laminar nucleus, was found to project to area 19 alone. The rabbit is not known to possess any region corresponding to area 19 of the cat, i.e. visual III, so that this explanation of the projection of the second field representation is not satisfactory. The evidence available at present is not, however, a very adequate basis for completely rejecting the possibility of visual III in the rabbit. It is alternatively possible that the arrangement in the rabbit is totally different from that in the cat and that the second field representation projects to visual II. Solution of the problem simply awaits the application of standard anatomical techniques.

Fig. 70 Dorsal view of L.G.N. showing the projection of the vertical meridia on the surface of the nucleus (page 112). Medio-lateral and antero-posterior coordinates are indicated. Black dots to the left indicate the plane of the coronal sections shown on subsequent pages. Nasal and temporal field coordinates are indicated by the prefix N and T respectively. Note the second representation of part of the nasal receptive field.

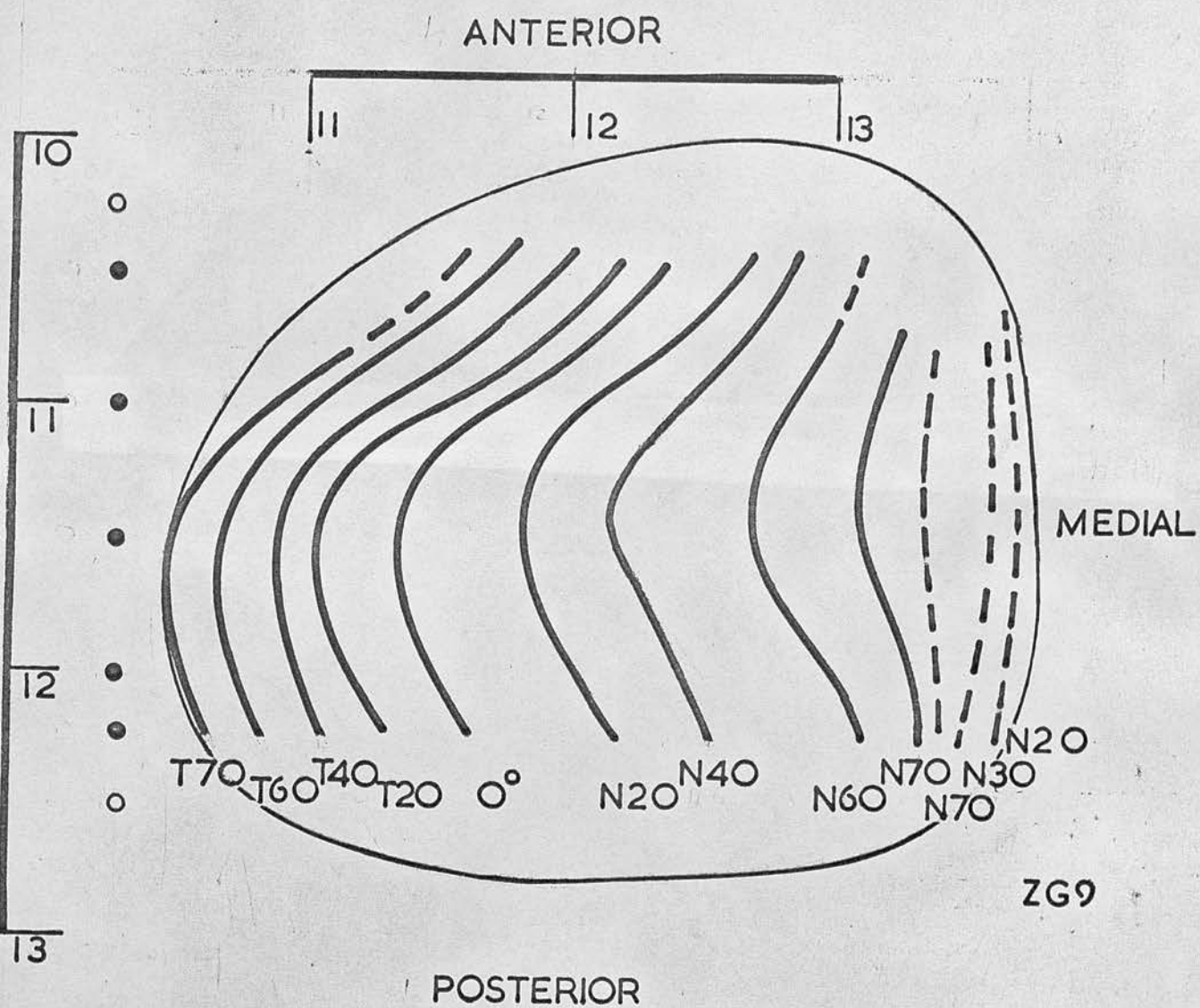


Fig. 71 Photograph of a coronal section 0.5 mm. anterior to the first coronal map.

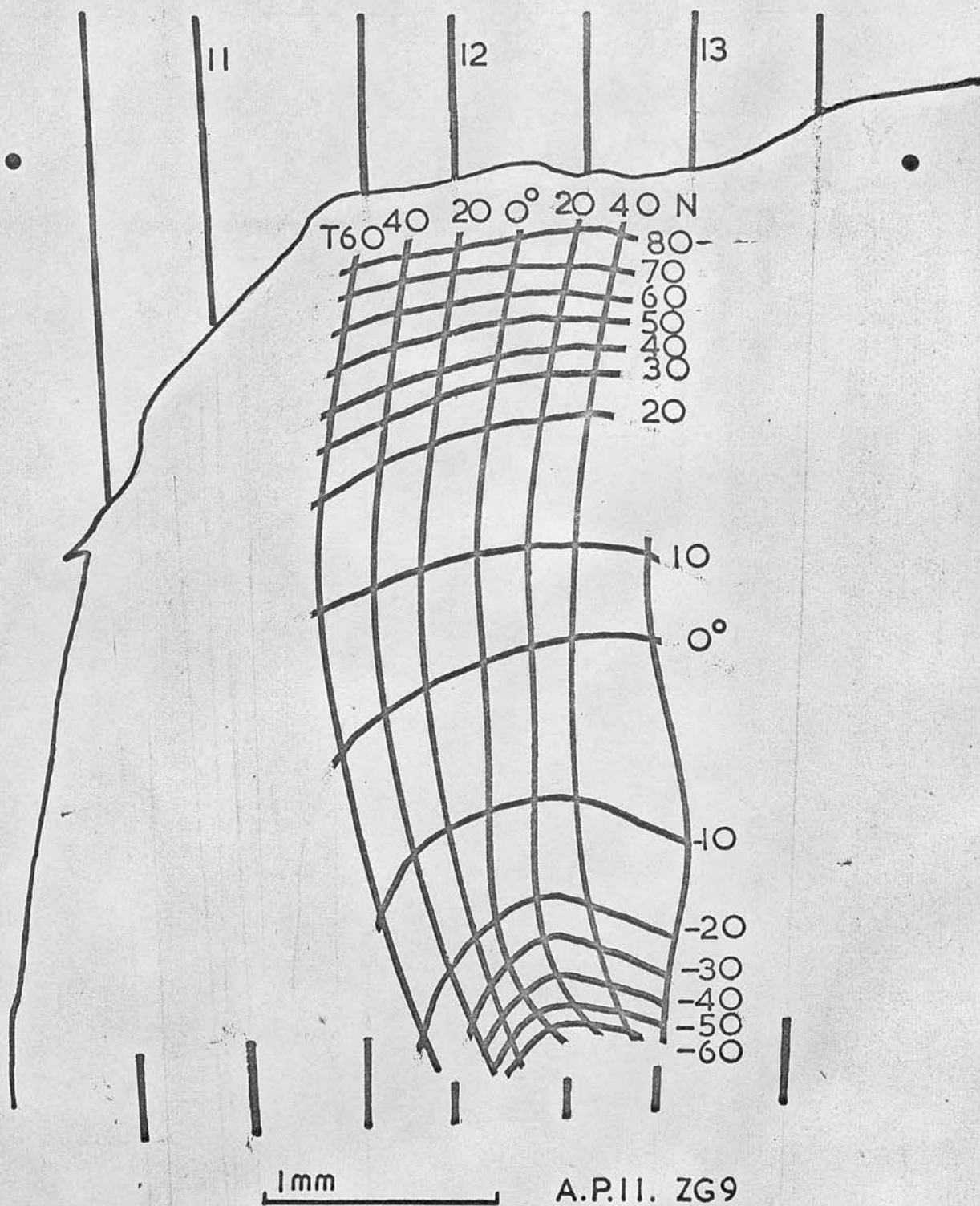
DORSAL

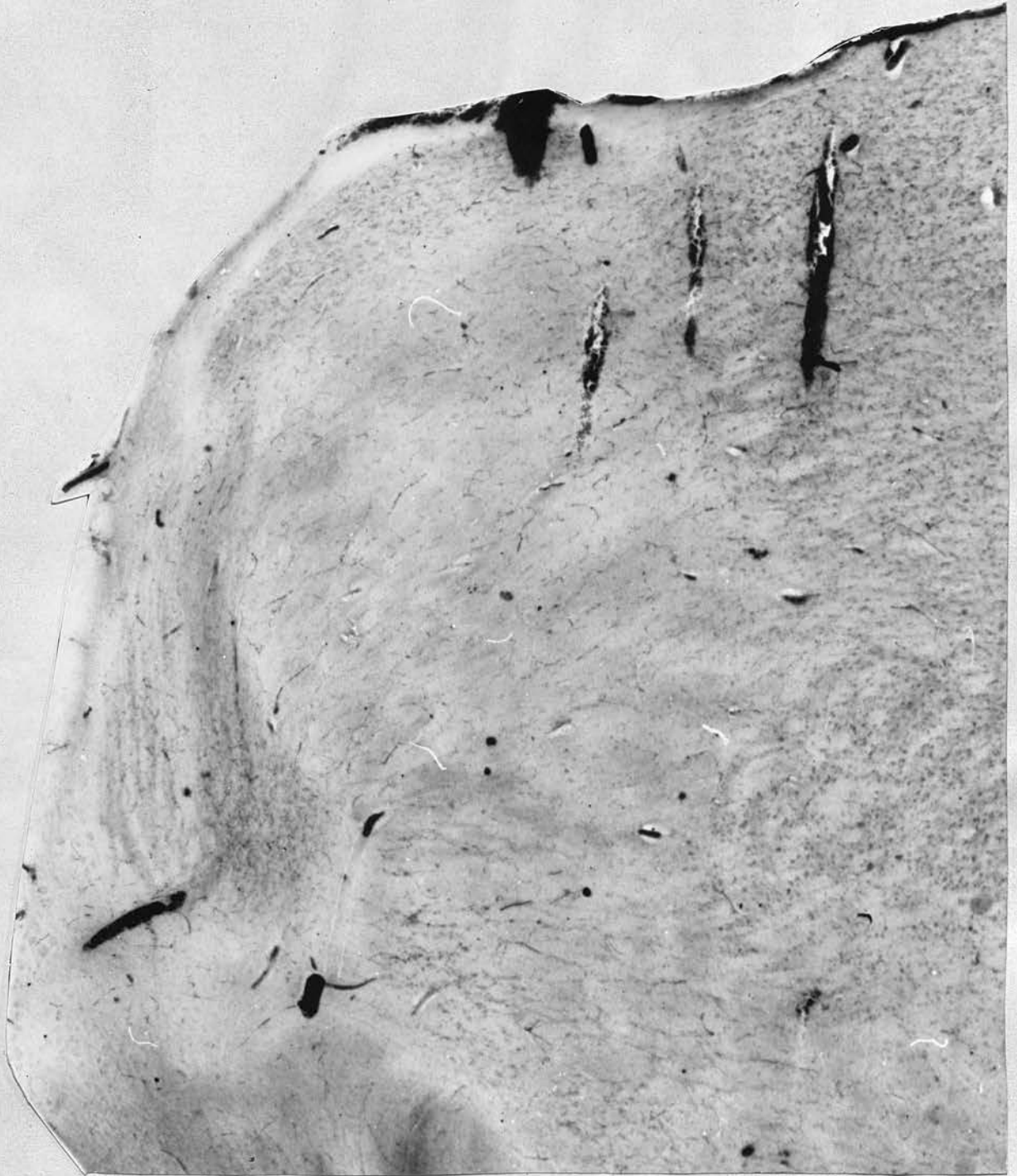
MEDIAL

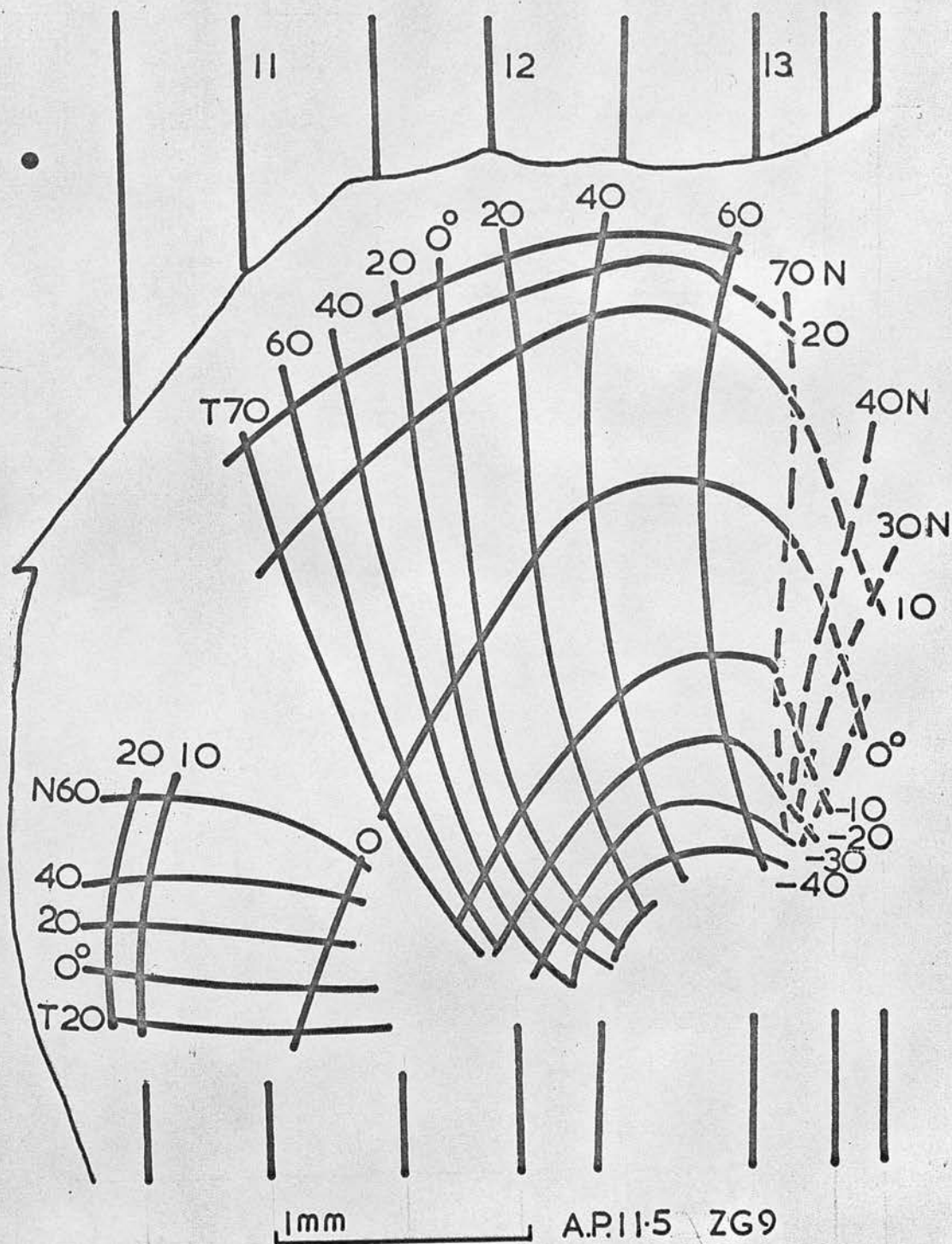
Fig. 72 (72b) - 76 (76b) see page 112f.

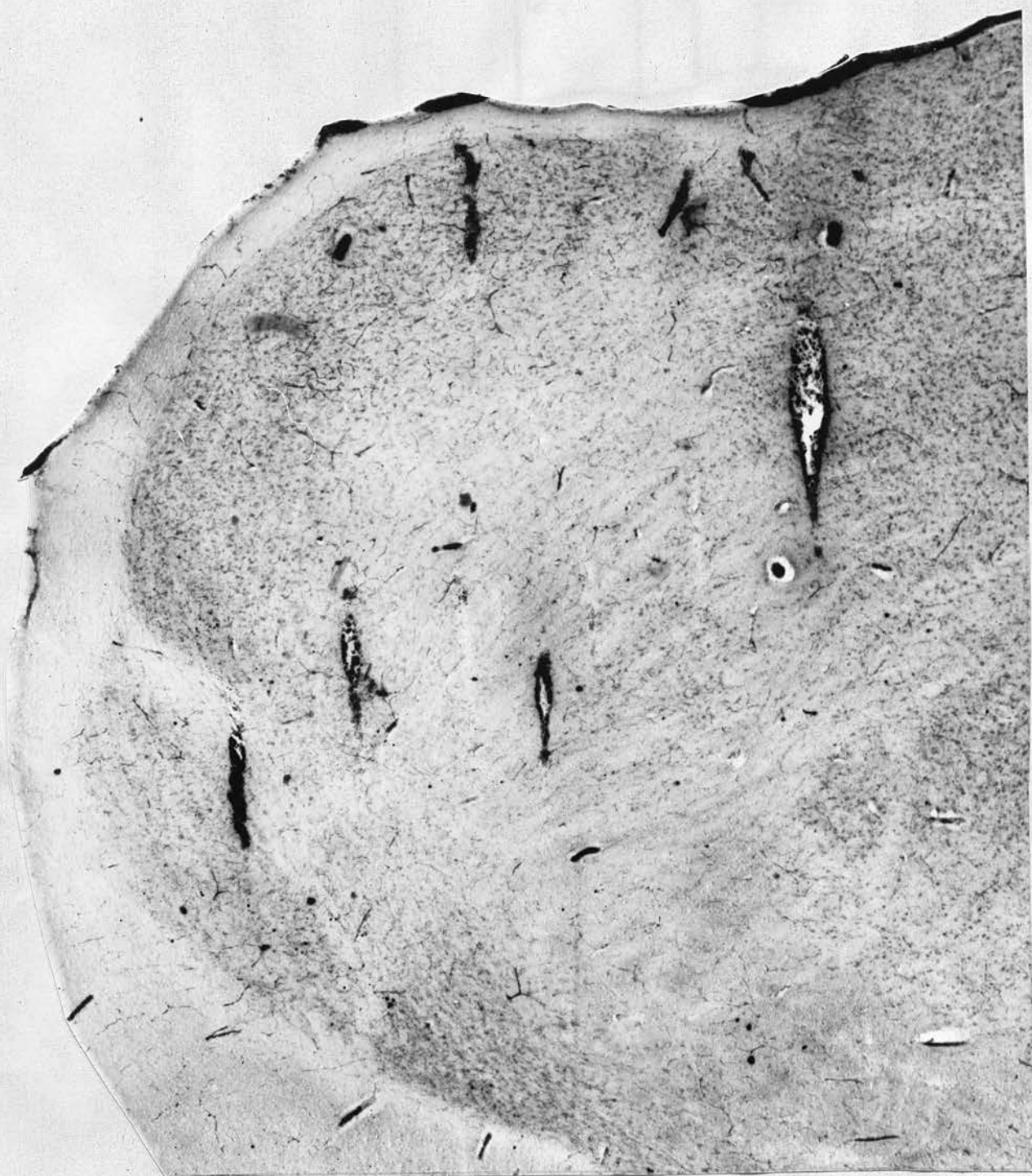
Vertical lines indicate the actual path of the electrodes as recovered histologically. The sampled points were marked on the electrode tracks with the corresponding visual field coordinates and the map drawn in over the outline of the corresponding coronal section. Black circles at the top left and right of the page indicate corresponding points for the accurate alignment of successive maps. The black squares to the right of fig. 72 indicate the spacing of the successive sampling points within the main body of the nucleus. It is not possible to show the sampling points and visual field projections of the points as this would take up too much space. The photographs show sections corresponding to the preceding maps. Note that the projection of visual field parallels into the nucleus follow the lines of fibre bundles.

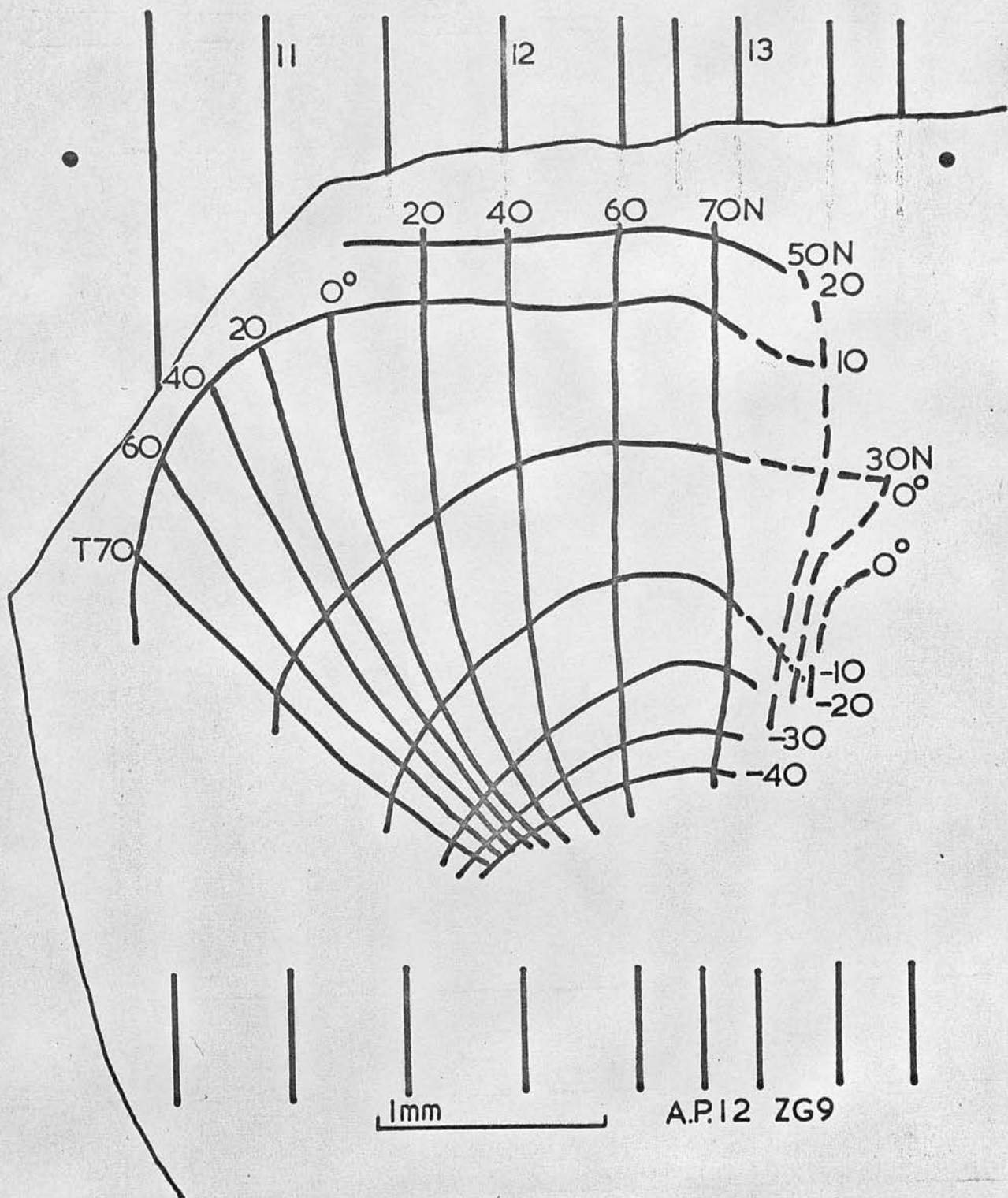
The representation of the visual field in the ventral nucleus of the L.G.N. in fig. 73 is to be noted as is the appearance of a second representation of the field in all maps except the first.





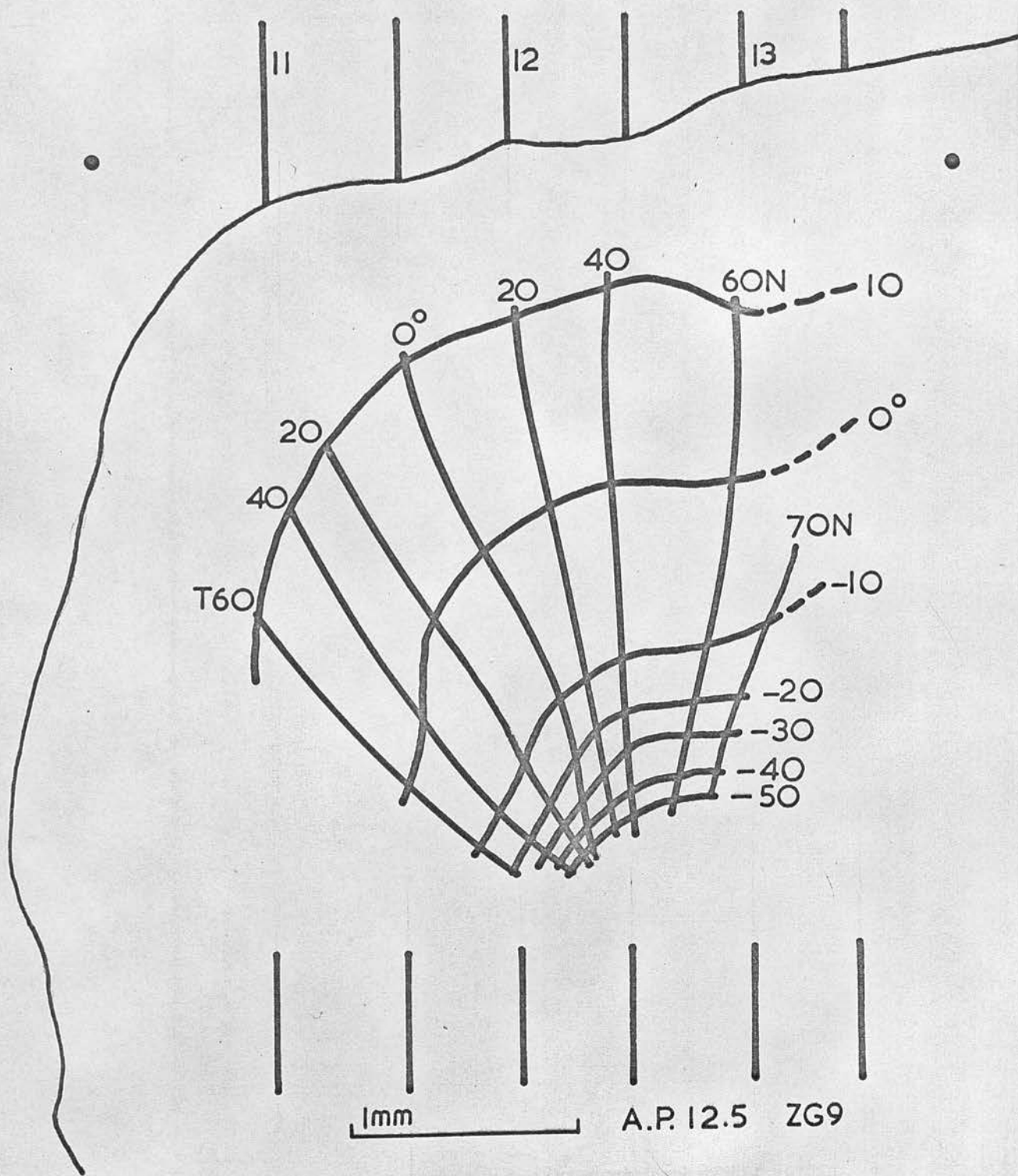


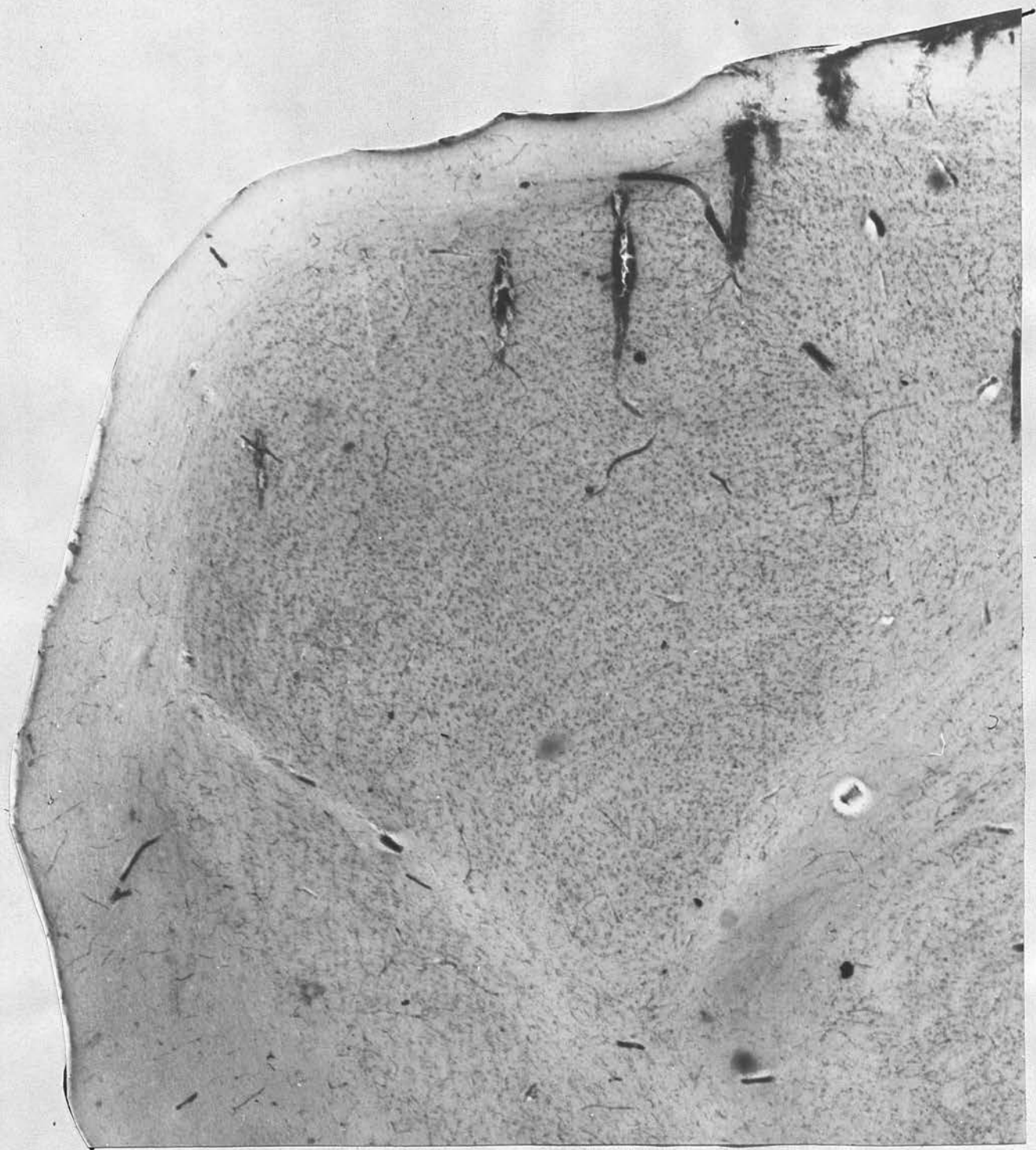


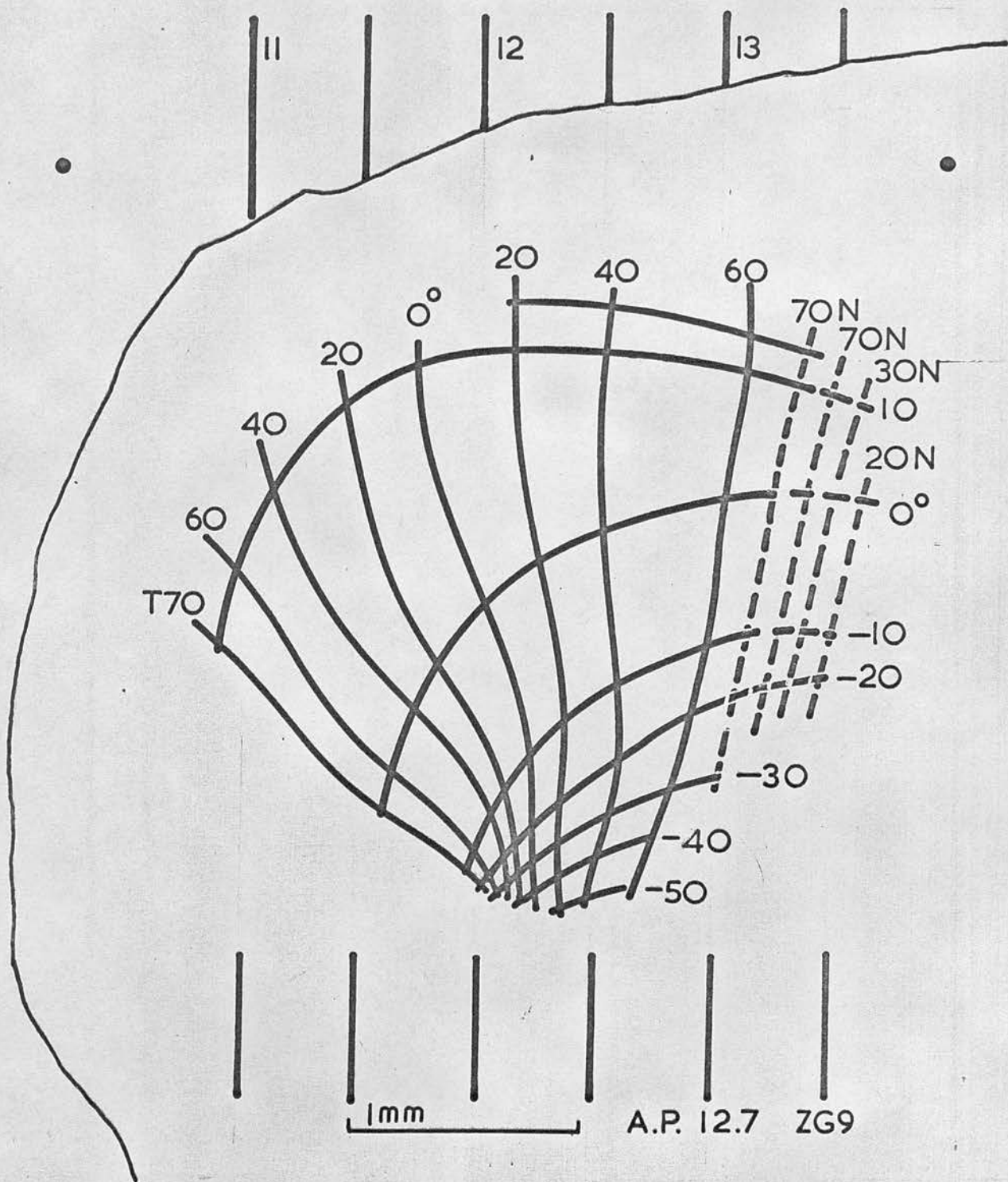




74b







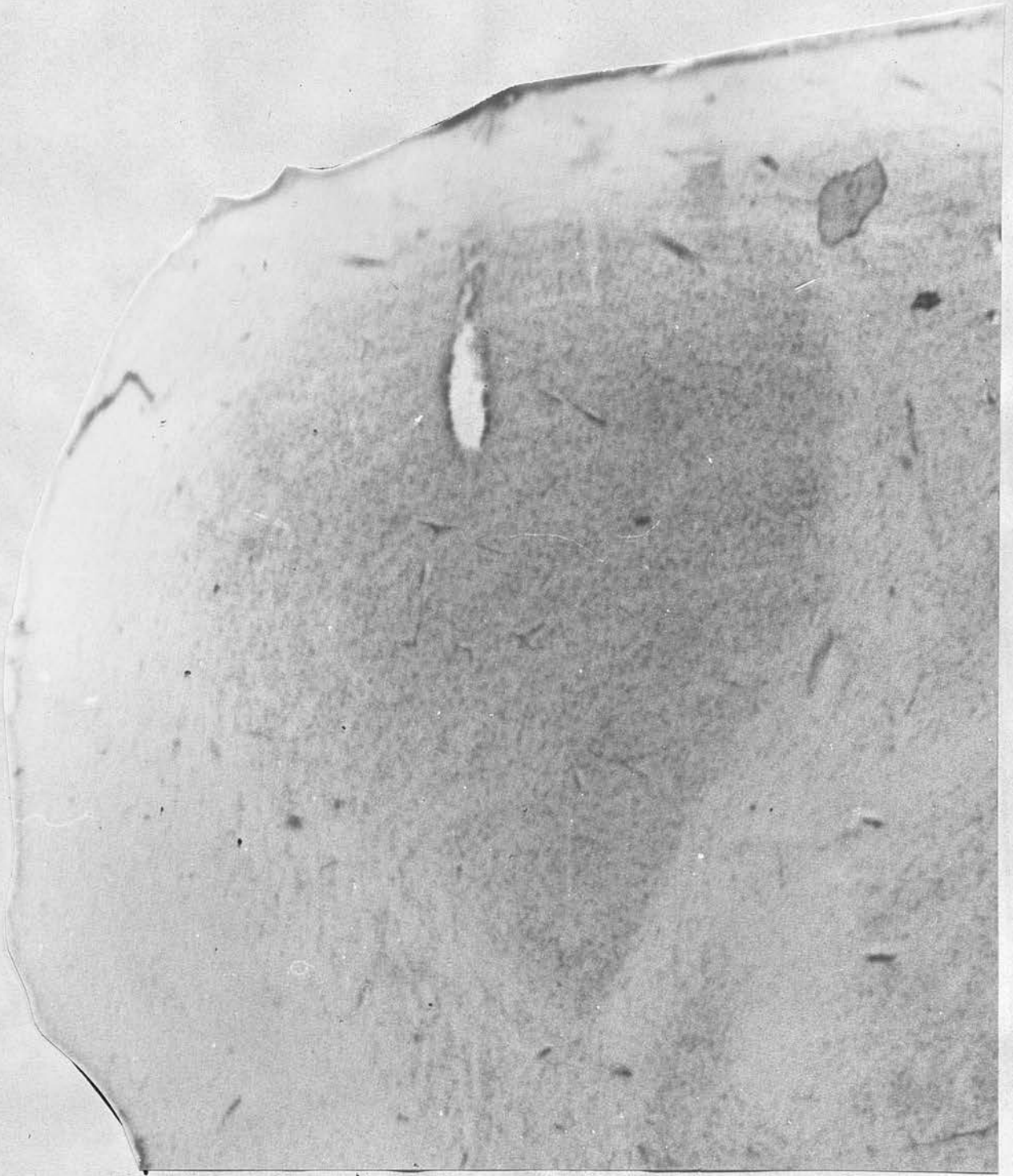


Fig. 77 Section 300 μ posterior of the final coronal map.

DORSAL

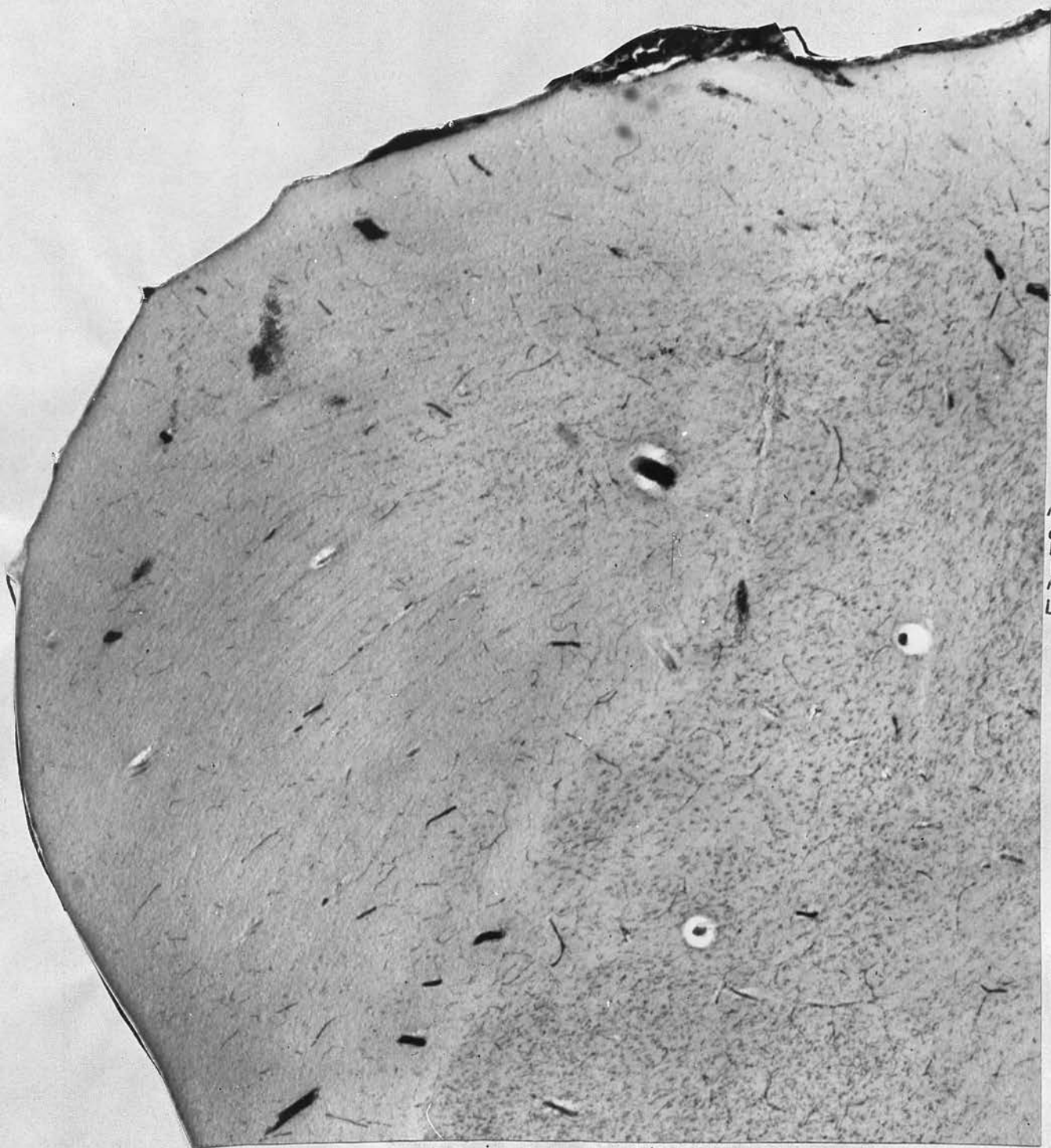


Fig. 78 Coronal map of the visual field projection into the L.G.N. of another animal showing similar arrangement to the preceeding case. Hatched area indicates the region from which a binocular response could be obtained. Note the second representation of the visual field in the medial part of the nucleus.

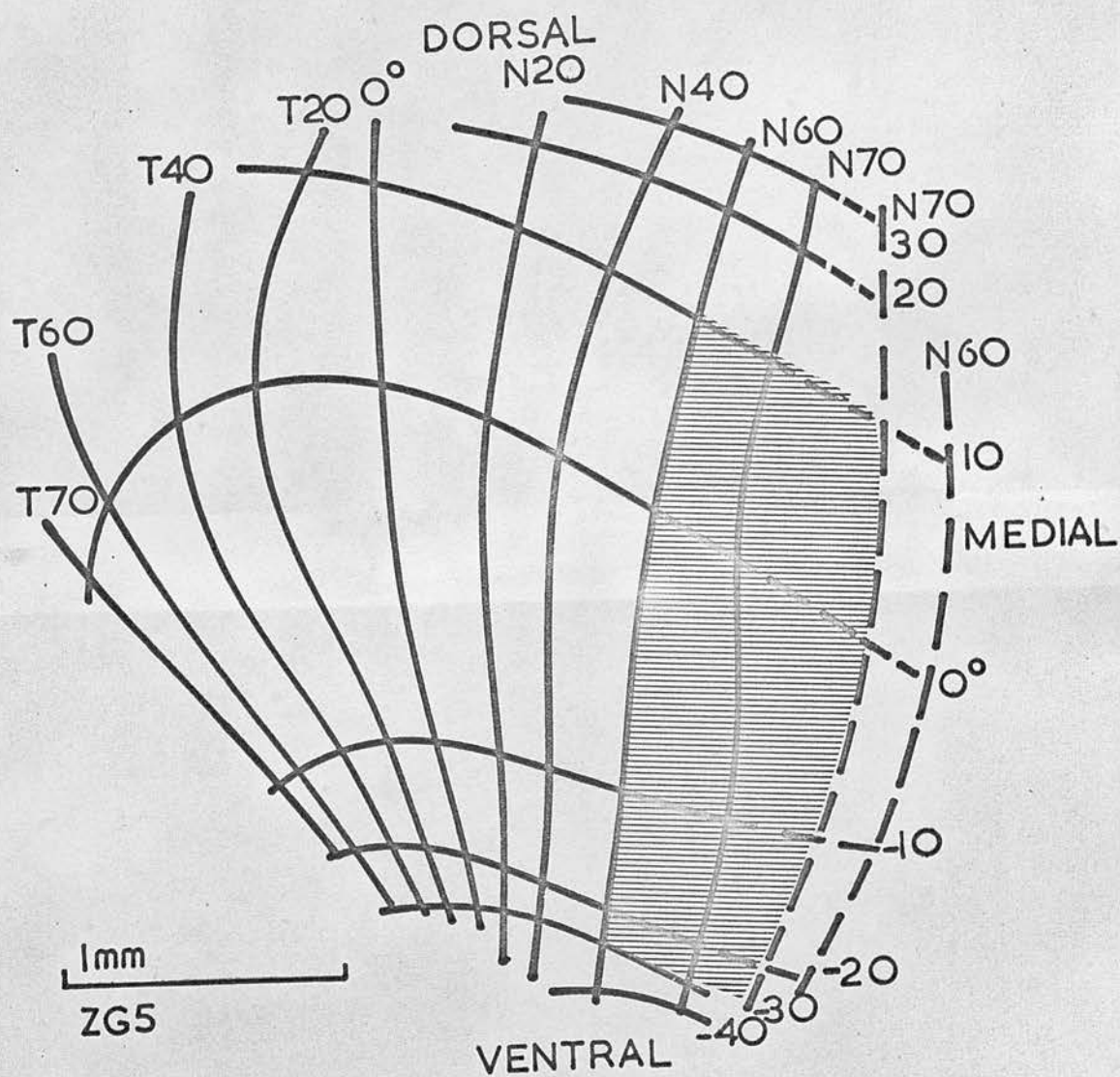
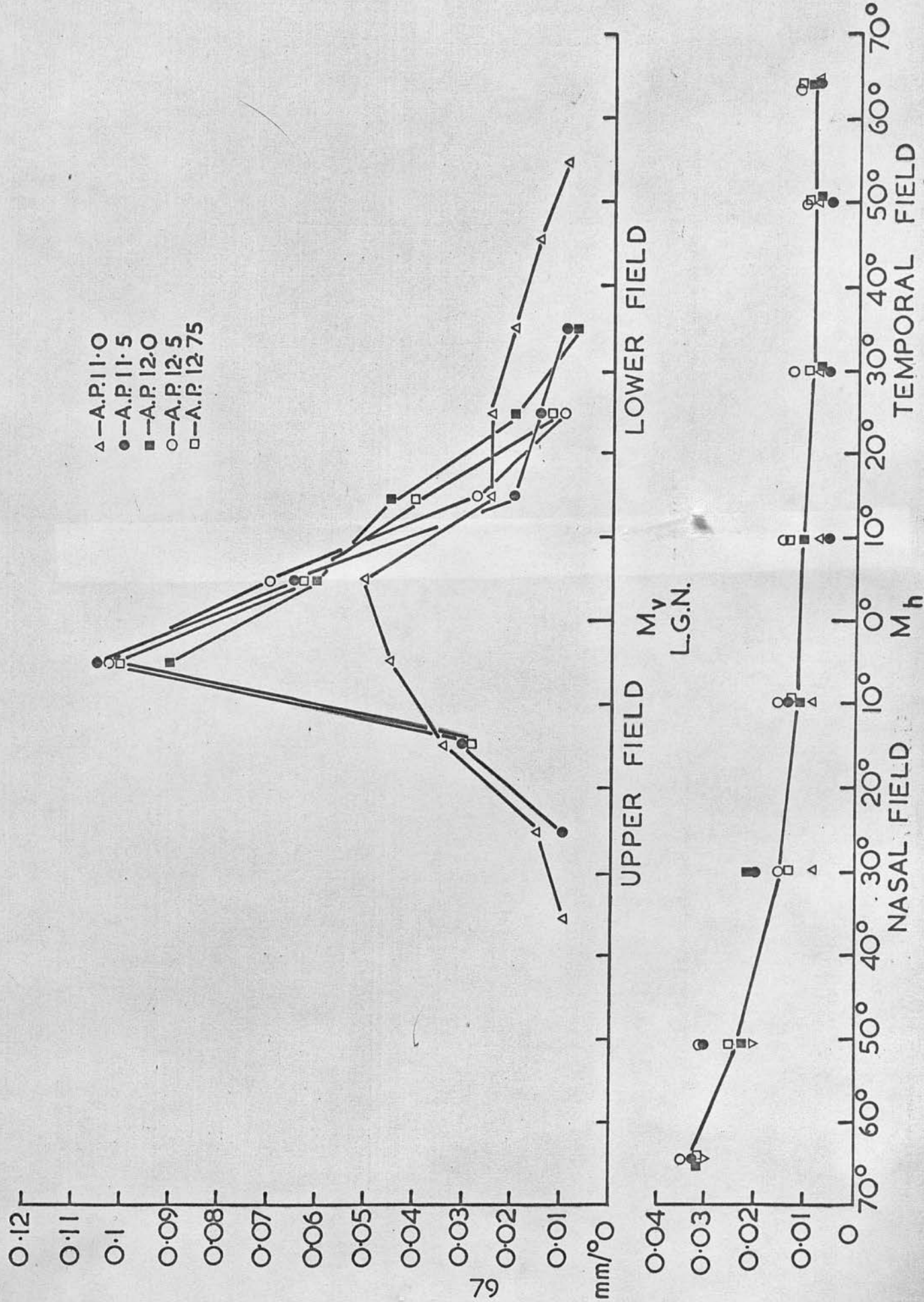
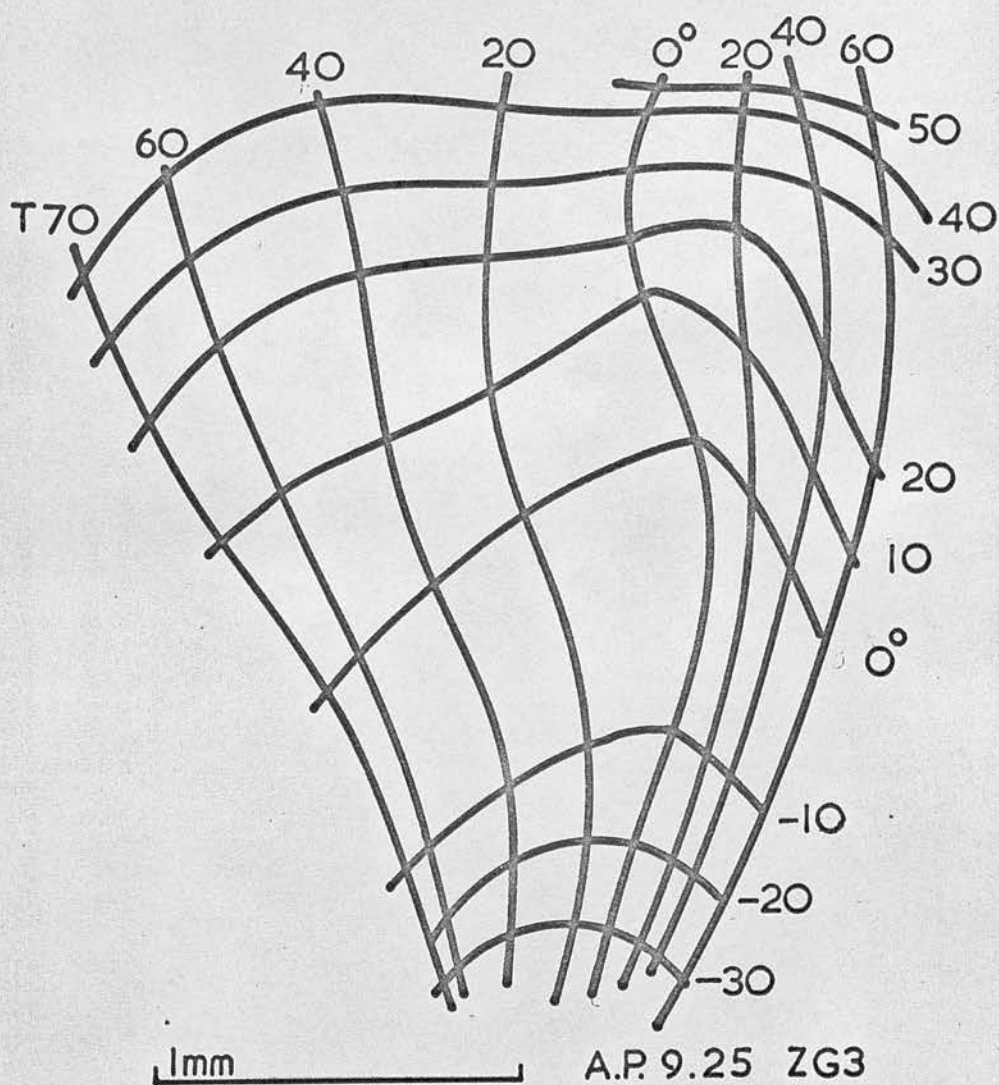
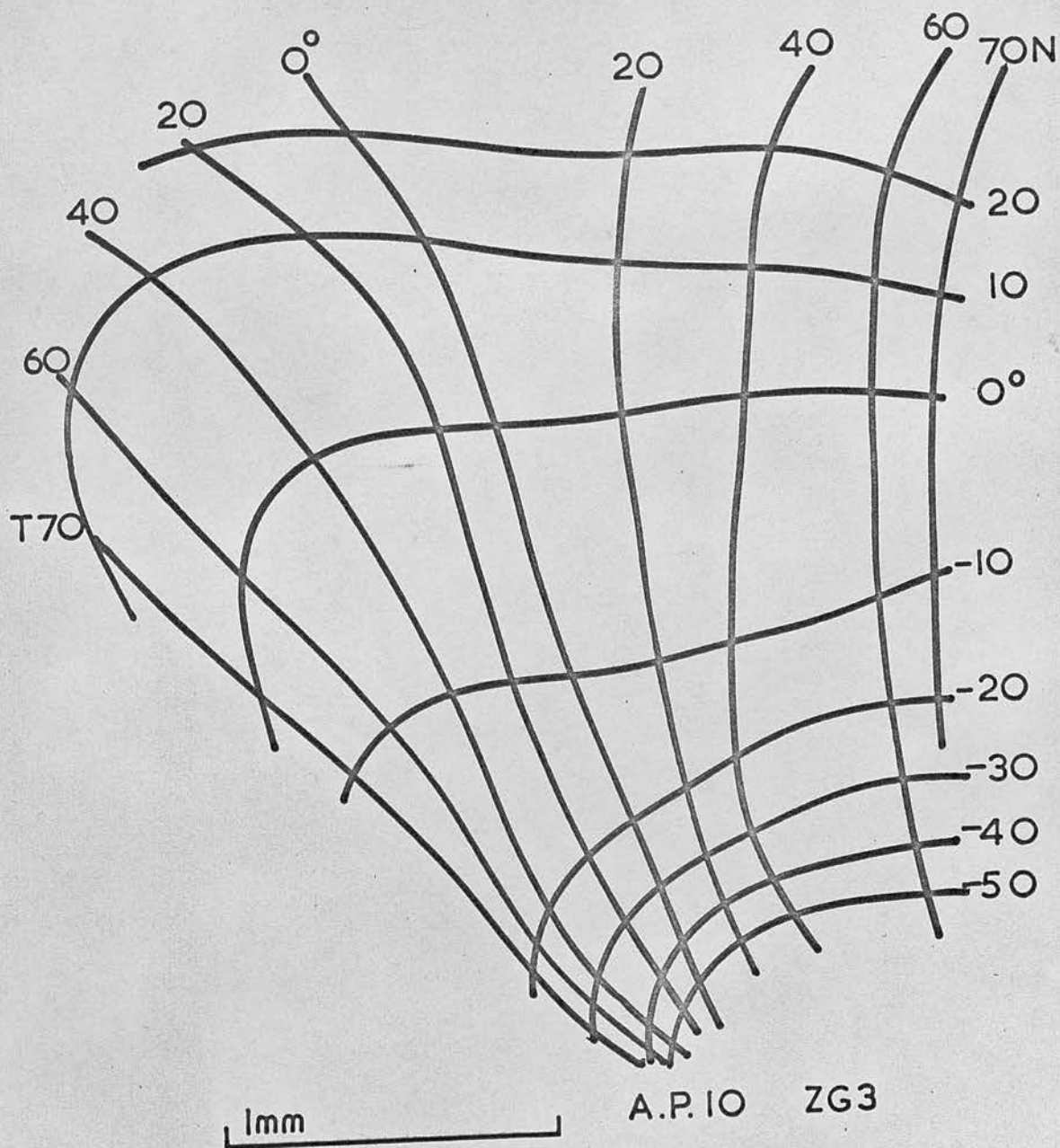


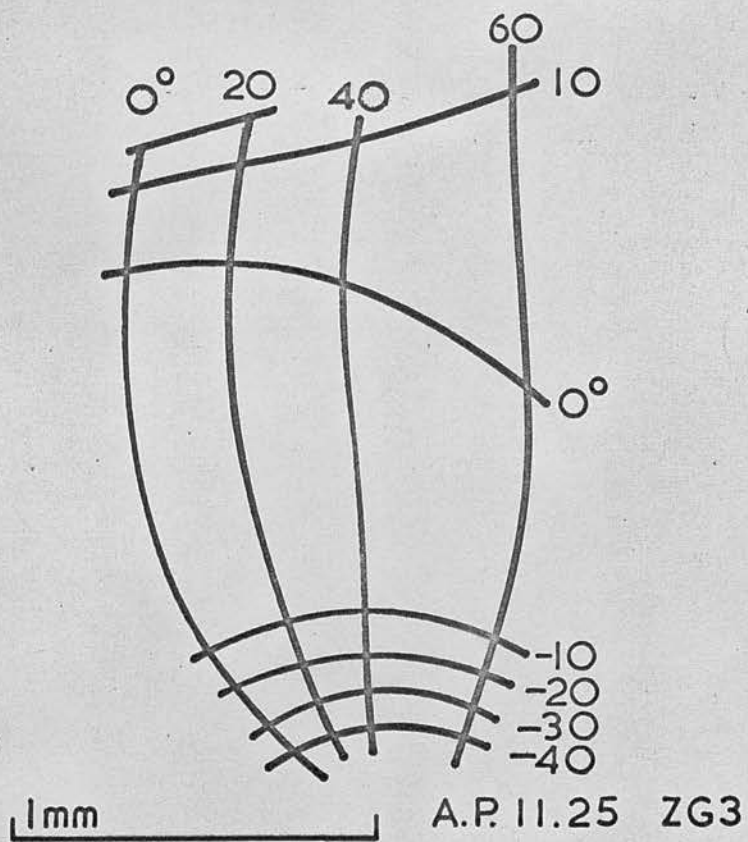
Fig. 79 Horizontal and vertical magnification factor plots for the maps shown in figs 72-76.



Figs 81 - 83 Coronal maps of the visual field projection into the L.G.N.
of another animal. For explanation see text on pages 117-118.







LGN SINGLE UNITS

No experiments in this series have been specifically devoted to the examination of the rabbit LGN single units. The literature contains only one report of the results of such an examination (Arden, 1963). In view of the fact that those results and conclusions are somewhat debatable it is felt appropriate to devote some space to the description of the single units encountered and examined during mapping experiments.

METHODS.

The usual methods for single unit analysis were employed (page 261). As the units described below were recorded during mapping experiments, it was always the case that they were obtained with a tungsten electrode and while the animal was under urethane anaesthesia.

RESULTS.

Single units of the LGN are often difficult to study because background activity tends to be high and to vary unpredictably. Too few units have been examined (about 30) for a sophisticated classification to be used so that they will be treated under the three headings below.

Small field units ($< 5^\circ$). The author has a very strong impression that the first unit to be encountered during a stab into the LGN has a high probability of being a large field off type. These units are inevitably near to the surface and sound like fibres rather than cells. It is most likely that they are optic tract units which are passing on to the superior colliculus. Somewhat deeper it is possible to record units which are identified as cells on the basis of pre-potentials, spike amplitude during electrode movement and injury discharge. Amongst the units identified as cells in the DLGN have been 2 directional units, 1 on-off adjacent unit and maintained on or off units and 1 on-off centre unit (4° centre). The units, apart from the on-off unit, were all similar in their properties to those of the optic nerve. It did appear, however, that the concentric types showed more developed peripheral inhibition. Seven other units similar to the above /

above have been examined but not identified as cells.

Medium sized fields (6-20°). These units showed variegated properties that were difficult to classify and rather changeable during examination. Such units were not encountered in the optic nerve. One of the simpler forms is illustrated in fig. 84. The expansion test shows a predominantly on centre with an off surround (fig. 84a). Flashes of one, three or twelve degree spots centred on the field led to a maintained on response (fig. 84b). During the off period grouped burst discharges were recorded. A twenty degree spot gave rise to an adapting and much reduced on discharge (fig. 84d). A quite good incremental brightening response was obtained to restricted illumination of the field (fig. 84e) but this was almost entirely eliminated by whole field (fig. 84f) illumination. It is difficult to tell whether a dimming response was obtained or whether rhythmic burst charges are simulating such an effect. The unit showed good flicker response (fig. 84g).

A marked characteristic of these somewhat larger fields (5-20°) was their greater sensitivity to moving stimuli than to stationary light flashes and in some cases the response habituated rapidly to a light flash while moving stimuli induced no habituation. Fig. 85a shows the response to movement of a 2° light spot through the 15° long, somewhat oval, field of such a unit. In contrast fig. 85b shows the occasional spikes occurring when the same light spot is flashed in the field. Slight movement produces a marked discharge and brings back the habituated response to the flashing spot.

Very large fields. A number of single units with very large receptive fields were recorded from the LGN. Such fields were encountered at the immediate posterior boundary of the dorsal nucleus. The units responded to on and off of a light flash and fired well in response to the neon. They all showed spontaneous firing and responded to the movement of card stimuli in their field. The receptive fields were less well defined than the long field units of the superior colliculus and surrounds could not be demonstrated. The fields were up to about 90°.60° and were most commonly found above or below the projection of the visual streak into the visual field.

DISCUSSION

The behaviour of single units in the rabbit LGN has been examined in detail by Arden and his co-workers alone. Diffuse light was used as a stimulus in the earlier work (e.g. Arden and Liu, 1960) but the stimuli utilised for the experiments reported in Arden's 1963 paper are more comparable to those used in the above work.

About $\frac{1}{3}$ of the cells encountered by Arden possessed fields some 6° in diameter and gave a uniform response to the flashing of a light spot at any point within the receptive field. It was not possible to demonstrate centre surround organisation in the case of the majority of the units studied.

The remaining $\frac{2}{3}$ of the cells possessed fields which showed 'complex' behaviour. These receptive fields were irregular in form and large. They often demonstrated some subdivision of the response form within the field. Spontaneous changes in the organisation of the receptive field occurred along with adaptation to repeated stimulus presentation. Most of the LGN cells fired best in response to moving stimuli rather than flashing light spots.

Arden interprets these results as indicating a high degree of convergence at the geniculate level in the rabbit. It is suggested that, in the 'less precisely organised' visual system of the rabbit, an equivalent process to cortical convergence in the cat is carried out in the LGN. There are good reasons, however, why this view should not be accepted.

Choudhury and Whitteridge (1964) report the recording of 13 small field units (2°), two 6° oval fields and four large field units (20° . 50°). The small units were obtained in the projection of the visual streak. Arden does not mention the presence of fields as small as 2° in diameter. The possibility remained that these small field units were optic tract fibres passing into the LGN. This argument is discounted, however, by the description of cells with such small fields encountered in the main body of the nucleus during the mapping experiments described above.

Further evidence for the presence of cells in the LGN with response characteristics similar to fibres of the optic tract may be obtained by consideration /

consideration of single unit work on the visual cortex which is reported in the next section. Single units with fields from 2-4° in diameter have been recorded from the rabbit visual cortex. The behaviour of these units is very similar to that of some of the optic nerve classes, e.g. they are directional or axial movement sensitive. It is irrelevant whether these units are efferent LGN fibres or visual cortex cells because, in either case, similar units would be expected to be present in the LGN.

The units of medium and large receptive field size appear to correspond more closely to those described by Arden (1963). The properties of the medium sized receptive fields were often very tedious to study during mapping experiments and these units were thus abandoned rapidly. It is thus not possible to compare findings of their properties with Arden's report.

It is to be noted that Arden (1963) used a visual stimulator which shone a light into the eye through a variety of stops bearing various sizes of hole. No correction was apparently made for near vision. It is possible that this experimental procedure gave rise to a great deal of light scatter which might make it impossible to adequately map the small field units of the visual streak projection.

The nature of the medium and large field units of the LGN remains to be elucidated. Such receptive fields are not found in the visual cortex. It is possible that some of these units represent the interneurons which are so plentiful in the LGN.

Figs 84 - 85 L.G.N. single unit responses which are described between pages 120 and 121.

SEE general notes following legend of fig. 43.

Medium sized receptive field of the L.G.N. The expansion test indicates an on centre and an off surround. The light spot expands through the centre region of the receptive field and illuminates the first photocoell. In the periphery a second photocoell becomes illuminated. Firing occurs during expansion through the ~~centre~~ and during contraction through the surround. See not iii facing figure 43.

Flash of a 1° spot on the field leads to a maintained response at on of light. Down of the monitor trace indicates off, up indicates on of the stimulus light.

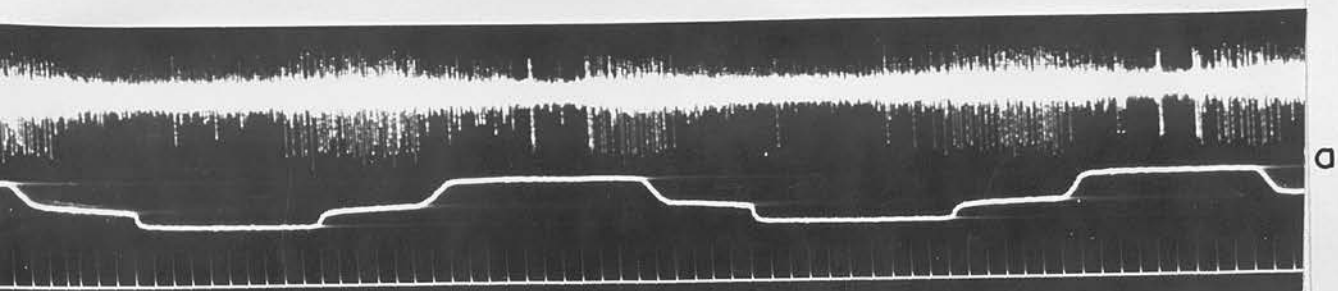
Similar conditions to the above but the spot is 12° in diameter.

The maintained on response is considerably reduced when the field is illuminated with a 20° spot. The conditions are otherwise as above.

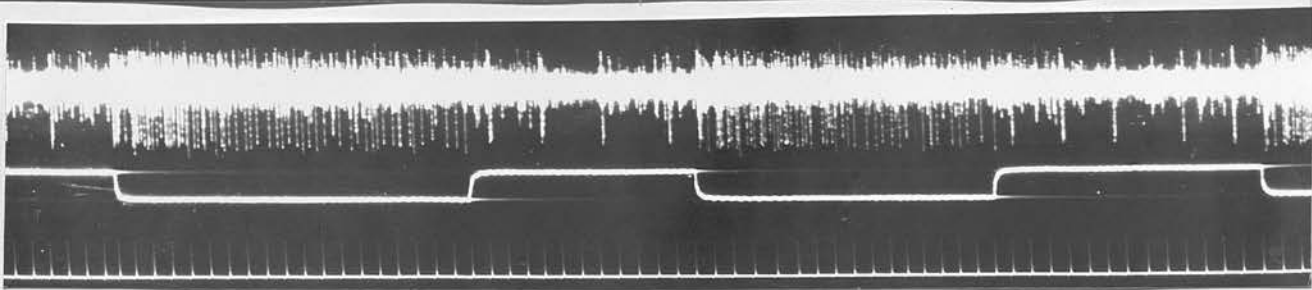
The unit gives a clear brightening response to a 5° light spot. Spontaneous bursts give the impression of a dimming response. Downward movements of the monitor trace indicates brightening.

Similar conditions but the brightening response is now elicited by whole field illumination of varying intensity. The response is considerably reduced.

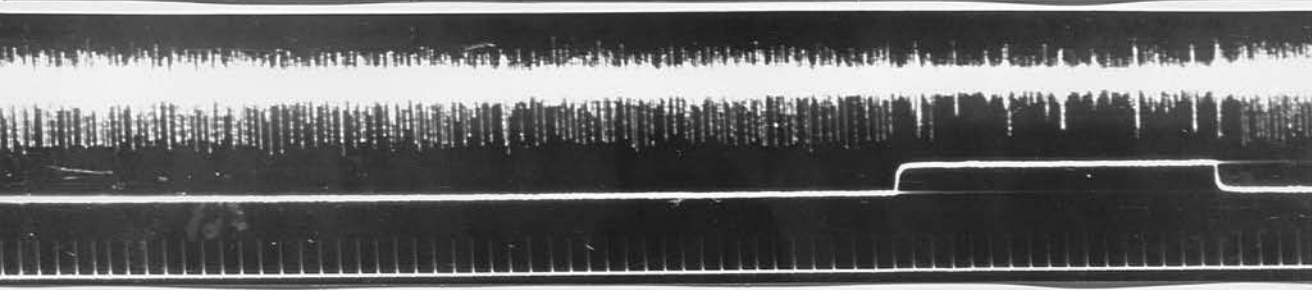
The unit synchronises its firing well with rapidly moving or flickering stimuli.



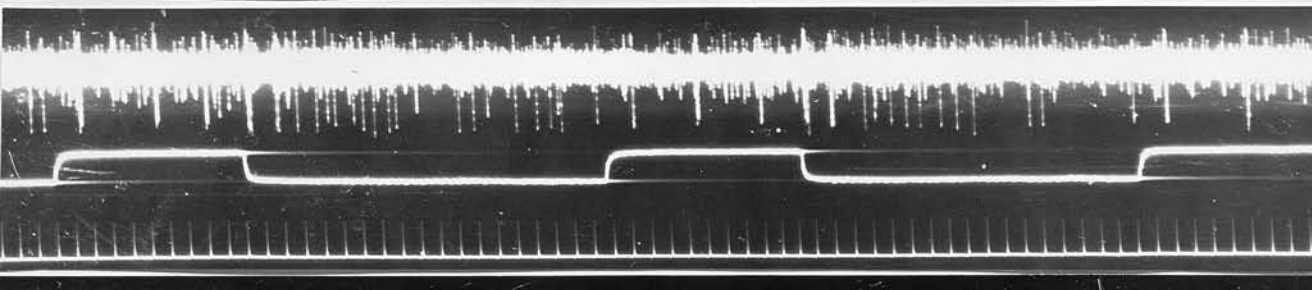
a



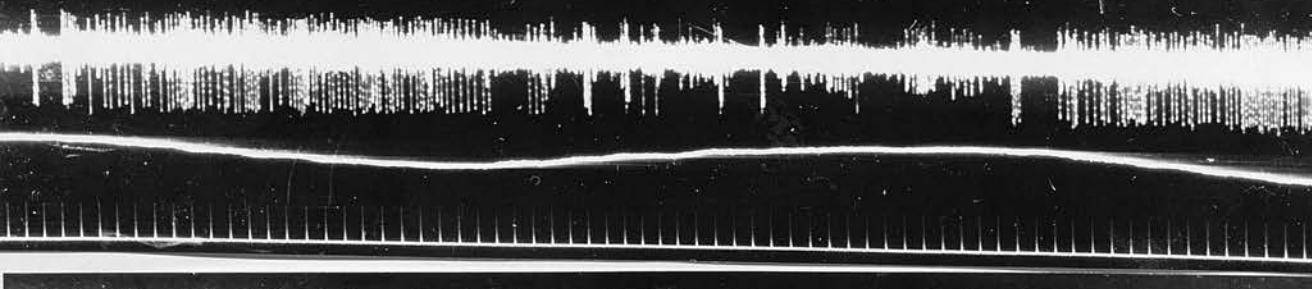
b



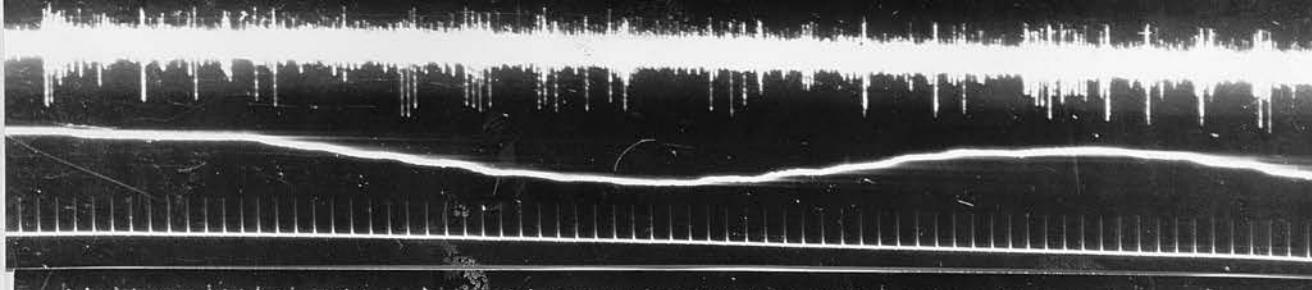
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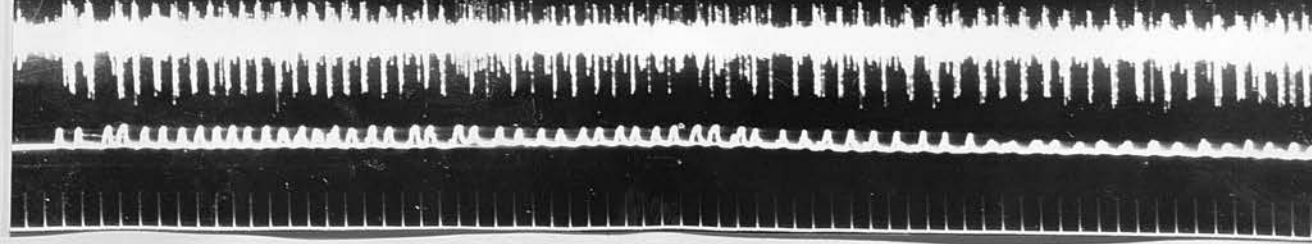
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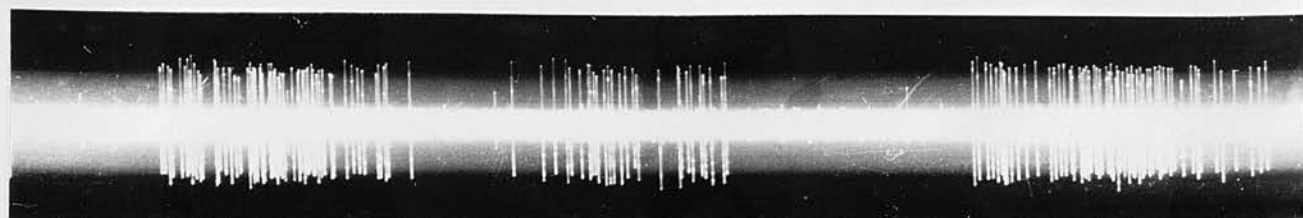
The photograph shows three bursts of firing obtained at each of three movements of a 2° light spot in the receptive field of a medium sized L.G.N. field. The monitor trace carries no information.

Flashing of the same spot evokes only a single spike after an initial burst of four spikes. The two periods of firing occurring between flashes indicated by the monitor trace arose when the spot was moved to a new point indicating that unit was not refractory to all stimuli. Down of the monitor trace indicates off of the light spot.

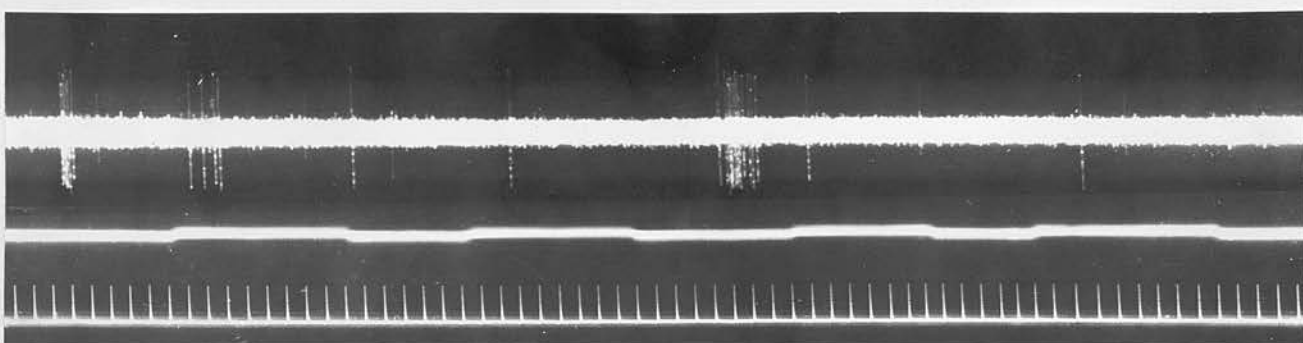
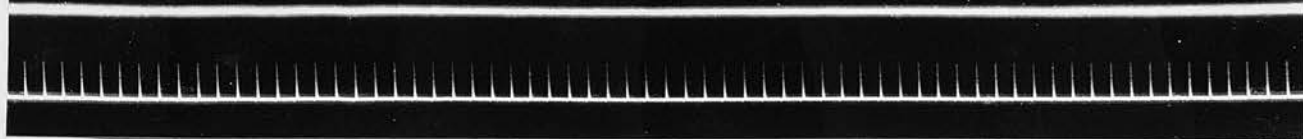
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a



b

CYTOARCHITECTONIC DEFINITION OF VISUAL CORTEX

The extent of the rabbit visual cortex was first determined cytoarchitectonically by Brodmann (1909) who designated it as area 17 on his map of the cortex. Area 17 was assumed to be homologous with the same area in the cat and primate in which it is also known as the striate cortex because of the prominent white fibre band of Gennari in the fourth layer. This stria, whose fibres are of unknown origin (Le Gros Clark, 1942), is not so readily observed in the cat as in the primate and appears to be absent in the rabbit. The application of the term 'striate cortex' to the visual cortex of rabbit (e.g. O'Leary & Bishop, 1938) is thus not based upon the appearance of the area in that animal but upon that of homologous regions in other species and is consequently best avoided.

Brodmann (1909) describes the rabbit visual area as being located at the posterior pole and on the dorsal surface of the hemisphere with its medial margin adjacent to the splenial sulcus. The area is shown as surrounded, except on its lateral edge, by a narrow band of cortex, area 18, which shows a structure intermediate between that of the regions bounding it on each side. The map of Rose (1931) is based upon similar criteria to those of Brodmann and shows a similar arrangement of area 17. The area 18 was, however, extensively subdivided into an anterior 'area parietalis quarta et occipitalis', 'area parietalis tertia et striata' and the 'area perstriata' which runs along the medial boundary. The lateral edge of area 17 is adjacent to a region termed the 'area occipitalis'.

The appearance of the rat visual cortex, as outlined by Krieg (1946), is similar to that of the rabbit. The area 17 is described as bordered on the medial aspect by an area 18 and on the lateral aspect by area 18a. The anterior region of transition to parietal cortex is homologised with area 7 of the higher animals. The area 18a is homologised with the area occipitalis of Rose's rabbit map but bears no structural relation to either the rat area 18 or Brodmann's area 18 in the rabbit. The identification of the lateral regions in the lower animals is a matter of some confusion.

In all forms higher than the rodents Brodmann (1909) generally describes two /

two occipital regions, 18 or area occipitalis, which lies adjacent to area 17, and 19 or area pre-occipitalis, which lies lateral to area 18. In the terminology of Elliot Smith (1907) areas 18 and 19 are the parastriata and peristriata respectively. The transition from area 17 to 18 is readily detected in most species but, even in man and the primates in general, the transition from 18 to 19 is more difficult to locate. Lashley and Clark (1946) refused to draw any distinction between the areas 18 and 19 of *Ateles* and *Macacca* on the basis of cytoarchitectonic differences. Von Bonin (1951) does not subdivide the parastriate area of *Tarsius*. Other workers, however, claim to distinguish between areas 18 and 19 in the cat (Otsuka & Hassler, 1962; Hubel & Wiesel, 1965) and monkey (Brodmann, 1909; Mettler, 1935). Lashley and Clark's position is probably extreme since other, functional, criteria indicate parcellations of function similar in topography to the areas designated in Brodmann's maps. The homology between the areas 18 in cat and monkey is suggested cytoarchitectonically by their similar position in relation to the readily homologised area 17 and the presence of a row of large cells in the layer III (Hubel and Wiesel, 1965). The similar position alone serves to homologise area 19 in cat and monkey. Projections and functional properties serve as better indices of homology than cytoarchitectonics in this case.

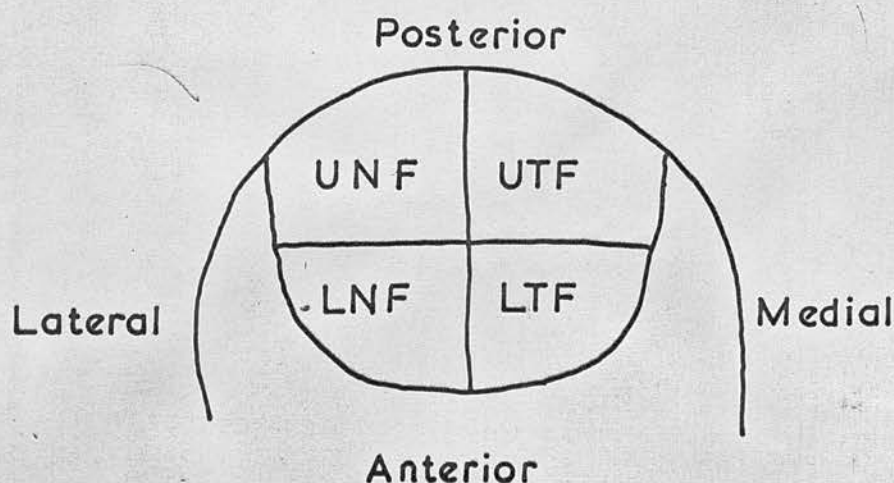
There is no difficulty in establishing the homology between the area 17 of the rabbit and other mammals but some confusion of terminology obscures the relationship of the other regions. Brodmann (1909) did not designate a lateral occipital area, corresponding to area 18 of the higher mammals, in the rabbit but indicated a direct contact between the limits of the visual and temporal cortex. The number 18 was reserved for the narrow band medial and anterior to the area 17. Rose and Malis (1965) have examined the criteria used by Rose (1931) for the differentiation of the cortical visual areas in the rabbit. The whole of Brodmann's area 18, or the peristriatum of Rose, was found to show properties transitional between the regions bounding it on each side. Brodmann's area 18 was thus incorporated into area /

area 17 rather than shown as a separate field. Brodmann was thus justified in his expressed reluctance to homologise area 18 in the rabbit with that in higher mammals. Rose (1931) corrected Brodmann's oversight in the matter of the lateral occipital region and identified the area occipitalis which lies in a position corresponding to area 18 of the cat. Under the present nomenclature it is clear that the area 18 of the cat is a quite different region to that in the rabbit. Krieg (1946) introduced the number 18a to indicate the homology of the area occipitalis of the rat to 18 of the cat. In view, however, of the absence of any indication of an area 19 in the rat and rabbit it must be considered whether the area occipitalis is equivalent to area 18 of the higher forms or takes the place of both area 18 and 19. Rose's (1931) choice of the term peristriate area for his medial division of Brodmann's area 18 must not be taken to indicate any relationship, such as is suggested by Elliot Smith's terminology, to area 19 of higher mammals. Until more is known about the function of the area occipitalis it is best to avoid the possible imputation of a false homology by deferring the designation of the region with the number 18.

TOPOGRAPHY OF THE RETINO-CORTICAL PROJECTION

INTRODUCTION

The first, partially successful, mapping of the retinal projection on to the visual cortex of the rabbit was made by Putnam and Putnam (1926). Localised cortical lesions were made which gave rise to degeneration in the LGN. Brouwer's map of the retinal projection on to the LGN was then used to determine the retino-cortical connection topography. The binocular field was described in an anomalous position and the cortical representation of the retinal quadrants requires a 90° clockwise rotation in order for it to come into agreement with more recent findings. It is usually stated that the findings of Putnam and Putnam are thus invalidated. It will be remembered, however, that the LGN map of Brouwer was shown to be somewhat incorrect by Choudhury and Whitteridge (1964) whose results have been confirmed and extended above. The use of the new LGN map to interpret Putnam and Putnam's results in experiments 1, 2, and 7 (1926) enables the following map of the retinal quadrants to be obtained. More sophisticated techniques confirm its outline.



The most detailed maps of the cortical visual field projection have been obtained by the determination of the position in the visual field at which

which a light flash elicits a maximum cortical evoked response for each of a number of systematically arranged electrode positions. The rabbit visual cortex map of Thompson, Woolsey and Talbot (1950) reveals, unlike the anatomically determined plots, the presence of a second, topographically arranged, visual area located lateral to the responsive region whose borders correspond roughly with those of area 17. This second representation of the visual field, VII, is a mirror image of VI and adjoins it at the laterally placed projection of the most nasal vertical meridian.

Thompson et al. found that a light in the visual field beyond the 70° nasal meridian would elicit no response on the contralateral visual cortex. The region of field from 70° to 90° was observed, however, to project to the ipsilateral cortex at points superimposed upon the contralateral representation of the region of field from the 50° to the 70° vertical meridia. This area of binocular projection was found in VI and VII. When the eyes are in their normal, converged, position, the region of cortex receiving the 20° ipsilateral projection will also receive, in its contralateral projection, a representation of the same region of field as observed by the other eye. It thus appears likely that the animal obtains some form of stereoscopic vision from this limited binocular field.

Choudhury (1963) has reinvestigated the work of Thompson et al. and confirms the general outline of their results but was unable to map VII. Choudhury's map of VI reveals an expanded representation of the visual streak and of the nasal region of the visual field. He states that Thompson et al. have not observed these points but a close examination of their map (fig. 86) reveals that the expanded nasal region is represented in their results but is masked by a change of scale. The amount of cortex representing the region from 20° to 30° (on their map) is the same as that devoted to the field from 30° to 60° in either VI or VII. The authors do not overtly refer to this region but observe the possibility of a second area of enhanced resolution in the temporal field. It is not clear whether they refer to the nasal expansion or simply the enhanced representation of the lower visual field as the first area.

A series of mapping experiments were carried out in order to attempt confirmation of Thompson, Woolsey and Talbot's description of VII and to resolve the discrepancies between their map of VI and that of Choudhury.

METHODS The major representation on the dorsal cortical surface and the overlying visual field projecting to a given point on the cortex was determined by the localisation of a number of single unit fields in each stab. The experimental methods were routine (p. 259) except in that the head was rotated around its long axis by some 30° in order to arrange that the projection of VII on to the plane at right angles to the electrode axis was not excessively reduced by the steep lateral margin of the cortex.

RESULTS It is thus possible to obtain quite accurate estimates of magnification. VI and VII were successfully mapped in the case of three rabbits; partial maps of the two regions were obtained in four other experiments. The dissection necessary to expose VII is considerable and adhesions of skull, dura and pia are often encountered and disturbed in which case extensive damage is done to the area. The skull was not removed from the margin of the posterior pole in order to avoid the possibility of damage to the lateral sinus so that this border of the brain may remain unmapped for 1.0 to 2.0 mm. from the edge. The results were transformed to the standard eye position with the optic nerve head projecting into the visual field at 20° below the horizontal. One such set of transformed data is illustrated below. Figures 87 and 88 show the points in the visual field corresponding to electrode positions in VI and VII respectively. Figure 89A is a plane projection of the electrode insertions in a plane at right angles to their long axis. The final map obtained from these results is shown in fig. 89B and is of representative form. The effects of cortical curvature in distorting the representation are not great. The map is clearly similar to that obtained by Thompson, Woolsey and Talbot /

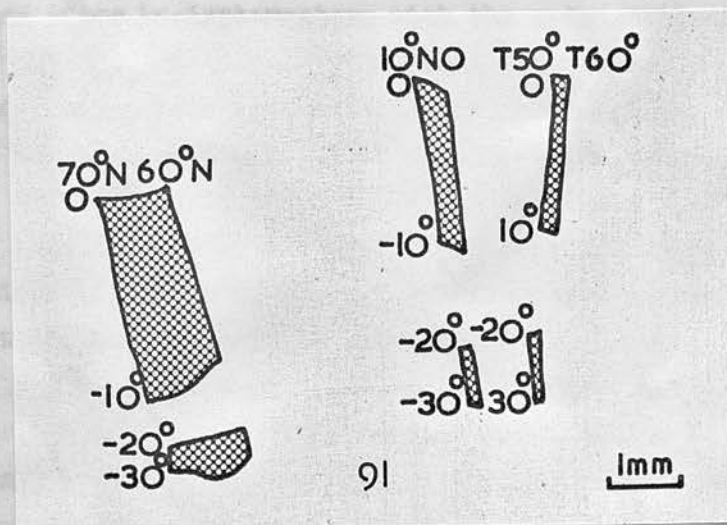
Talbot. The V_{II} representation is topographically arranged. V_I and V_{II} show an expanded nasal representation but Choudhury's description of a magnified visual streak projection is confirmed. No expansion of the temporal visual field projection has been observed. The lower visual field receives the major representation on the dorsal cortical surface and the overall orientation of the vertical and horizontal coordinates agrees with that described by Thompson et al. The junction, or decussation, line which separates V_I and V_{II} lies, however, more nearly parallel to the splenial sulcus in this map.

Cortical Magnification Factors. It is intended in this section to refer only to the map of V_I . V_{II} shows a similar topography but the number of electrode insertions into the area is inadequate for quantitative description. It is thus possible to obtain quite accurate estimates of magnification factors directly from the map of the cortical surface projected on to a plane because the mediolateral curvature introduces compression of the representation by more than 10% only in regions in and beyond the temporal portion of V_{II} .

Figure 90 shows a plot of the cortical magnification factor along the vertical meridian which passes through the optic nerve head and along the projection of the visual field equator. It is unfortunate that the map has not been able to be continued into the region of the upper visual field for the absence of points prevents the comparison of the vertical magnification factor plot with that of the colliculus. It is clear, however, that the vertical magnification factor along the chosen meridian changes in a similar fashion to that of any of the other meridians in passing from upper to lower field. This feature was used to obtain an estimate of the magnification factor between the $+10^\circ$ and $+20^\circ$ parallels which had not been successfully determined on the chosen meridian. The $+20^\circ$ parallel is, however, represented at the nasal meridian of V_I and the value of the magnification factor determined at this point has been included in the plot in the region represented by the discontinuous line.

The /

The plot of the horizontal magnification factor along the projection of the visual streak is shown in fig. 90. The value of M decreases progressively from the extreme nasal to temporal field representation. These variations of the magnification factors in both horizontal and vertical directions have the effect of making the area and form of the cortical region devoted to the representation of a 10° by 10° element of visual field rather variable. Figure 91 shows the form of such regions selected from nasal, central and temporal field representations. It is apparent that 10° wide elements of the cortical visual field representation lying between the 0° and -10° parallel occupy areas ranging from 0.8 (nasal) to 0.15 (temporal) of that occupied by the corresponding retinal regions. The areas devoted to the representation of elements not in the visual streak projection are considerably reduced relative to the corresponding areas on the retina. In the lower temporal field a 10° by 10° element may occupy on the cortex an area 1/28 of that of corresponding retinal region.



CALLOSAL PROJECTION TO THE VISUAL CORTEX

INTRODUCTION

Nauta and Bucher (1954) have described lesions to area 17 in the rat as giving rise to degeneration in the lateral 1/3 of the contralateral area 17 and in the adjoining medial portion of area 18a. Area 18 received no such callosal connections. No lesions were made exclusively to area 18a so that it is not known whether this region projects to the contralateral hemisphere. More recently Heimer, Ebner and Nauta (1967) report that area 17 in the rat receives relatively few degenerating callosal fibres after hemispherectomy but the projection to a strip presumably corresponding to area 18a is very dense.

In the cat, Hubel and Wiesel (1965) have traced Nauta degeneration from very limited lesions in area 17 to the contralateral areas 18 and 19. They were unable to exclude the possibility of degeneration in contralateral area 17.

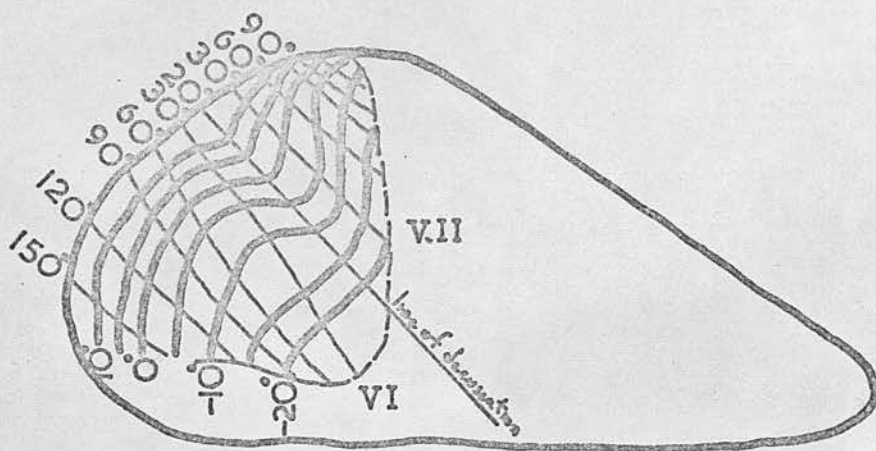
Ebner and Myers (1965) have compared the pattern of Nauta degeneration in the cortex after hemispherectomy with the cytoarchitectonic map of Otsuka and Hassler (1962). Callosal projections were found to area 18 but 19 and 17 were almost completely free of signs of degeneration.

Doubt has been cast upon these results by Wilson (1966). He has pointed out that the 17/18 boundary in the results of Hubel and Wiesel is more medial than is usually the case. If some error has been made in the identification of the cytoarchitectonic boundary, then the callosal connections would terminate within area 17. Wilson also points out a clear error in the results of Ebner and Myers whose dorsal projection of the cat cortex shows the different pattern of degeneration to that in the set of cross sections accompanying the paper. In the cross sections, the degeneration is seen to extend up to the medial border of the lateral gyrus which places it well within the margin of area 17 on Otsuka and Hassler's map.

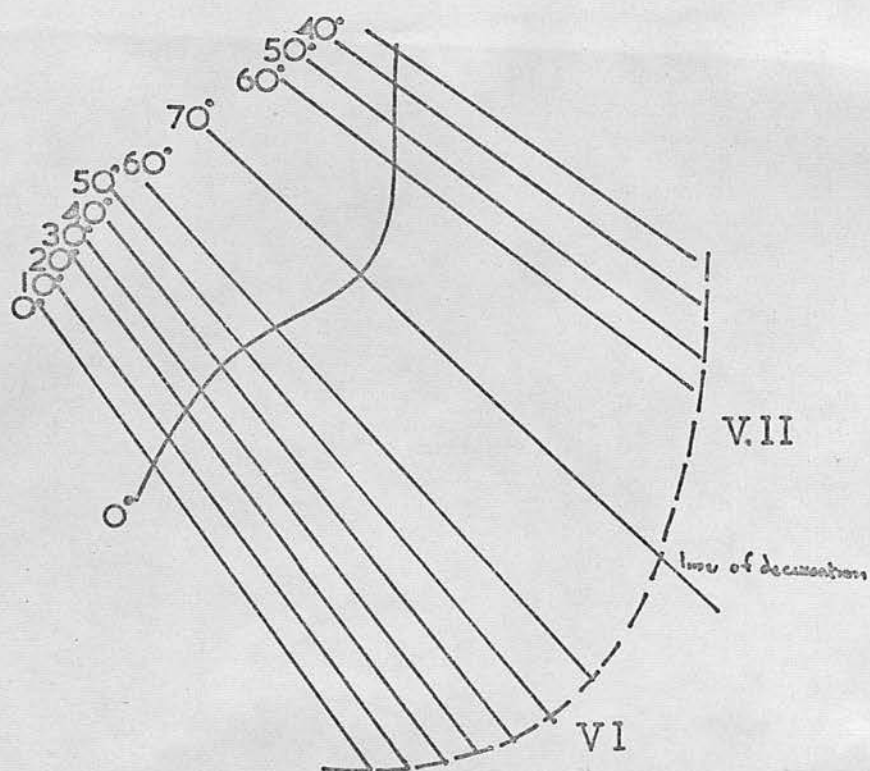
Wilson's own work supports the above criticisms of Hubel and Wiesel's and Ebner and Myers' conclusions. Limited lesions to visual I were found (Wilson, 1966) to give rise to degeneration within a region about the corresponding point on the contralateral hemisphere. Limited lesions in VII (pinprick) /

Fig. 86 A. The projection of the visual field on to the rabbit visual cortex after Thompson, Woolsey and Talbot (1951).

B. The same map in schematic form with the meridia coordinates changed to emphasise the expansion of the nasal field representation. See page 128.



A



B

Fig. 87 Points in visual field which are represented in the primary cortical visual area at each of the electrode insertions shown in fig. 89. Each line of connected points represents a line of insertions running medio-laterally on the cortical surface. The arrow indicates the region represented at the most medial and most posterior electrode insertion shown in fig. 89.

CORTEX VI

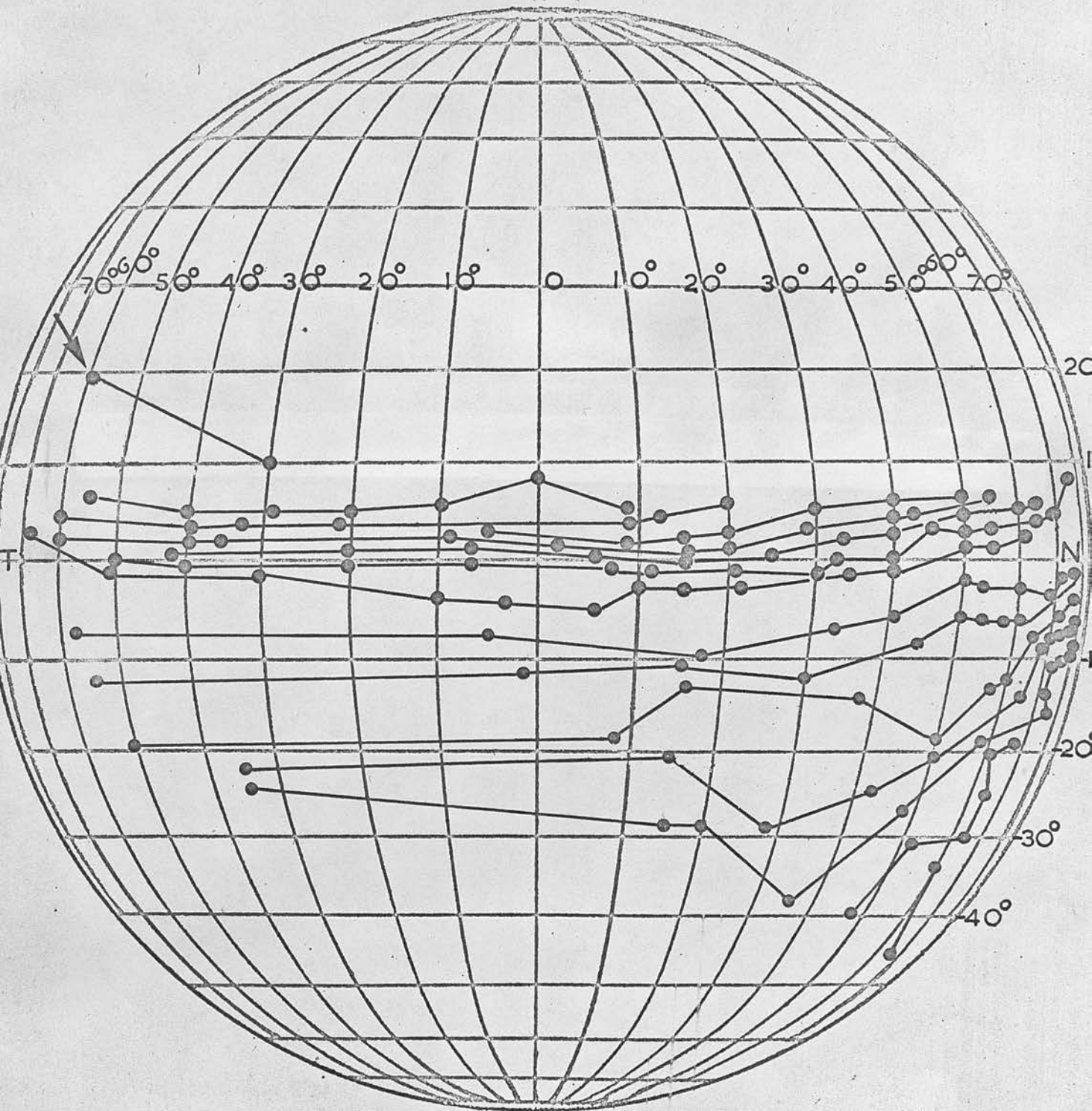


Fig. 88 This figure is similar to the above but shows the regions of visual field represented in VII of fig. 89.

CORTEX VII

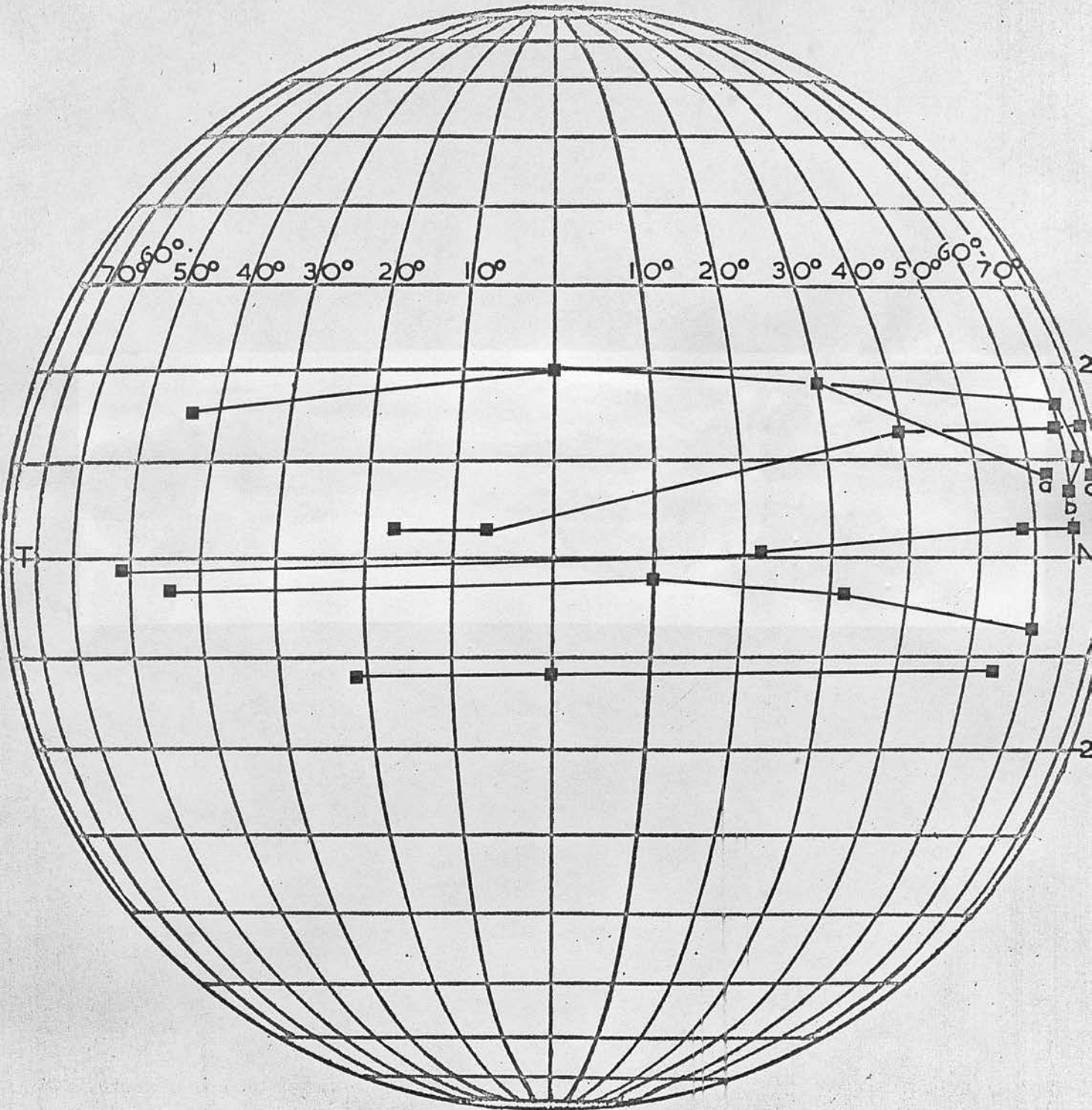


Fig. 89 A. Shows the matrix of electrode insertions which enabled the construction of the map of fig. 89B. White circles indicate that no visual response could be obtained from the region indicated. Black circles represent insertions in visual I, black squares represent insertions in VII.

B. Map of the visual field projection on to the rabbit cortex obtained from the preceeding data. D is the decussation line or boundary between VI and VII. The central vertical meridian is indicated by a heavy line in VI and VII. Note the expanded representation of the nasal field in VI and VII and the predominance of the representation of the region of visual field from 10° to -10° .

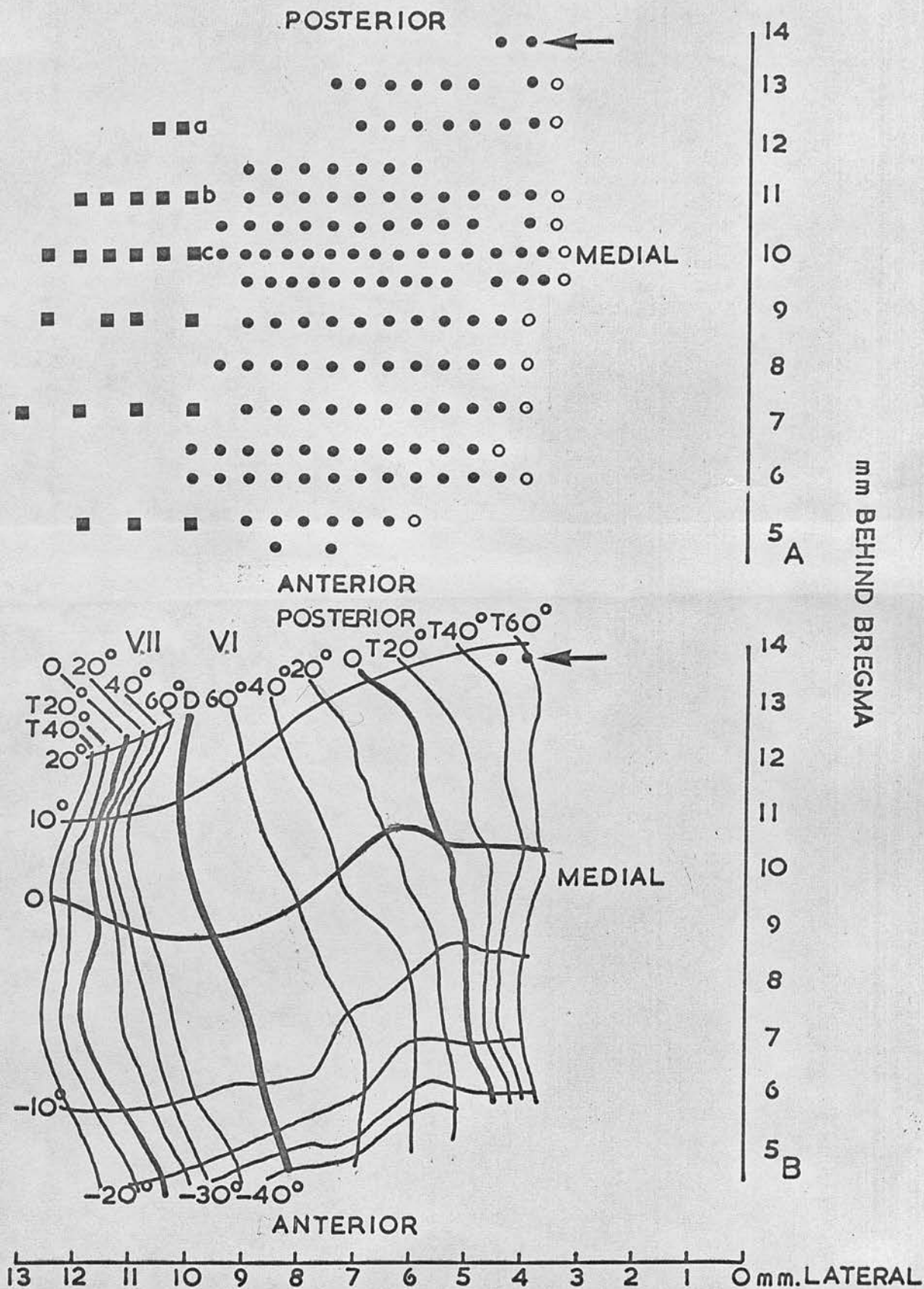
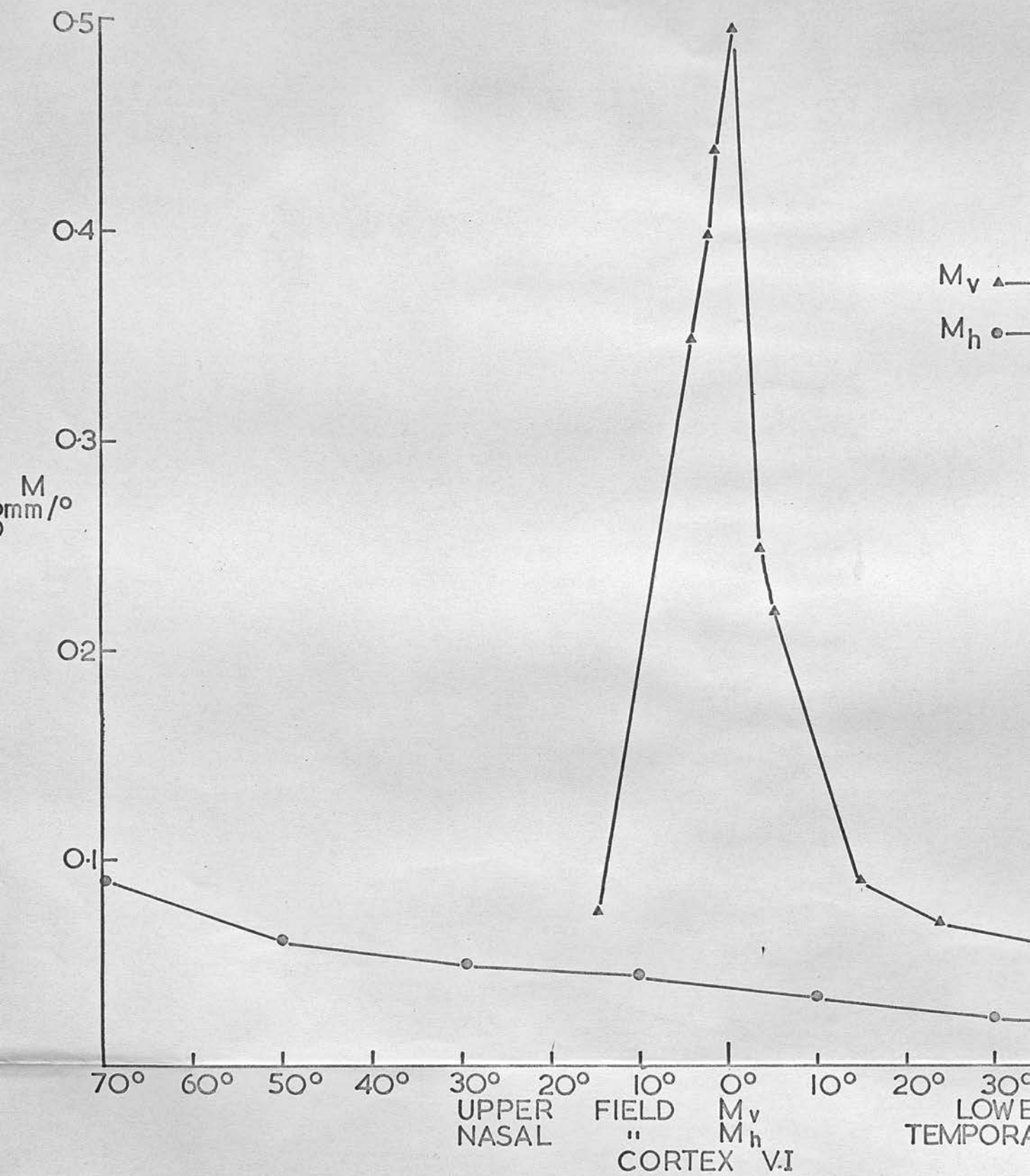


Fig. 90 Horizontal and vertical magnification factor for visual cortex.



(pinprick) were found to project to the corresponding contralateral region. Comparison of the results with the cat cortical map of Otsuka and Hassler (1962) reveals the lesions in VI were definitely within area 17 and thus that this region projects through the callosum.

In summarising the results obtained in earlier work (Myers, 1962), Myers (1965) describes degenerating fibres to be present in area 17 of the rhesus monkey brain, after hemispherectomy, only in a very narrow zone which is one to two millimetres wide and borders on area 18. Around its whole extent area 17 is in contact with a narrow, 2-3 mm. zone of cortex, which corresponds to part of area 18. It is important to note this concession of the presence of a callosal projection to the area 17, which indicates a similarity of organisation with rat and cat, for those interested in phylogenetic comparison may be misled by Myers' reiteration of the statement 'Area 17 of Brodmann exhibits almost total absence of commissural fibres'.

Comparison of the diagrams showing callosal terminations in rat, cat and monkey with the electrophysiologically determined maps of the visual regions reveals that the callosal terminations lie along the most nasal vertical meridian of the VI/VII junction. Experiments were undertaken in conjunction with Dr. M. Wilson (University College, London, who performed the three operations and carried out Nauta preparations) in order to determine the relation of the callosal terminations to the visual field projection on the cortex of rabbits (Hughes and Wilson, in preparation).

METHODS

The visual area was removed with a sucker from one hemisphere of each of three rabbits anaesthetised with nembutal. 5-10 days later the animals were again anaesthetised and perfused with formol saline. The caudal 15 mm. of brain was cut in the coronal plane on a freezing microtome. Sections cut at 30 μ were stained at 0.6 mm. intervals with cresyl violet and the Nauta method (Wilson, 1968). The position of Nauta degeneration was marked on the sections with a felt pen and they were then projected at a /


a magnification of x 3 and drawn. Maps of the degeneration were constructed by measuring the distance of the degeneration from the midline, perpendicular to the mid-sagittal plane.

RESULTS

The pattern of degeneration in the three brains was similar. A dense band of degenerating fibres was found to run from anterior to posterior through the region of visual cortex. The fibres entered the grey matter in a radial fashion. Few penetrated beyond layer IV. Figure 92A shows three of the brains in dorsal view and indicates the position of the degenerating fibres.

DISCUSSION

The cytoarchitectonic maps of Brodmann and Rose suggest that the visual cortex of the rabbit extends beyond the posterior pole to the tentorial aspect of the brain. Thompson et al. (1950) and I have recorded occasional responses to visual stimulation from this region but it has not yet been systematically mapped. It would be expected that the band of callosal fibre degeneration would extend to the posterior margin. The sectioning plane in the present experimental series makes the reconstruction of the tentorial surface very difficult but there are hints that degenerating fibres are present in a continuation of the band.

The  fig. 92B shows the VI/VII map described earlier. It is clear that the band of callosal fibre terminations falls on the border between VI and VII. It appears possible that the region containing degenerating fibres may be coextensive with the 20° binocular region of VI and VII but this would best be determined electrophysiologically. The relation of the callosal projection to the VI and VII representation is thus very similar to that in the rat, cat and monkey. In all three animals it appears to be linked to the integration of the visual field across the decussation line. In the cat, and the monkey, the visual field is split by the chiasma decussation across the region /

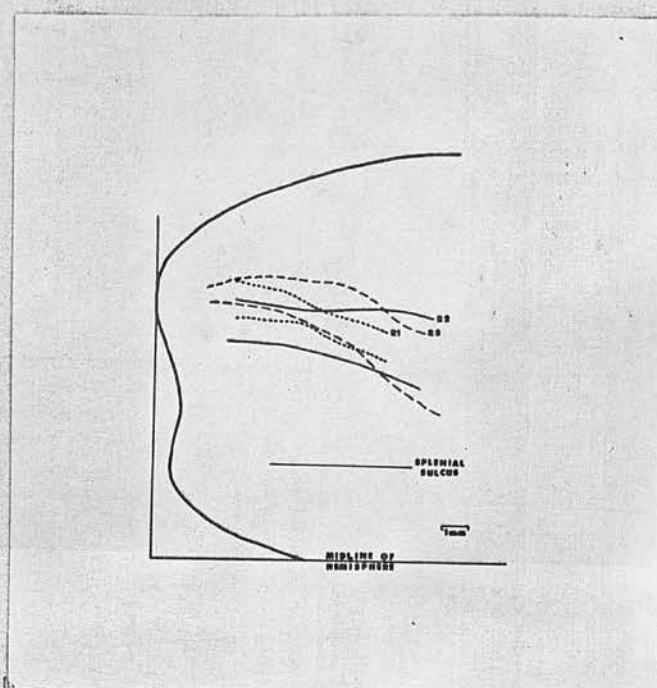
region of most distinct vision so that demands upon the callosal projection may be greater than in the rabbit.

The relation of VI and VII to the region of the callosal terminations is clear. The relationship of the callosal projection to the cytoarchitectonic boundary between areas 17 and occipitalis is less readily decided. The cresyl violet stained sections show a clear boundary between area 17 and an adjacent region in which layer Vb becomes scattered with cells and layer VI thins markedly. Adjacent Nauta stained sections are somewhat shrunken so that the most satisfactory results have been obtained by comparison of drawings of the sections made at slightly different magnifications in order to compensate for shrinkage. Figure 93 shows the appearance of one such pair of Nissl and Nauta stained sections from a region 8 mm. in front of the posterior pole of the cortex. The coincidence of the cytoarchitectonic boundary with the region of Nauta degeneration is clear and indicates that the decussation line, callosal projection and 17/occipitalis border are coincident as they are in the rat, cat and, possibly, in the monkey.

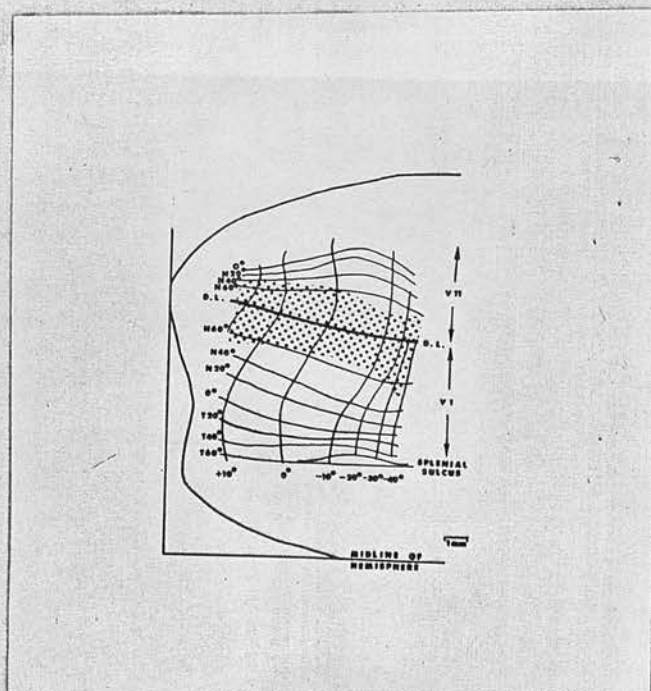
region of most distant vision and is thus probably a more complex system than in the rabbit.

Fig. 92 A. Dorsal view of the distribution of the band of degenerating transcallosal fibre terminations subsequent to the removal of the opposite occipital lobe. Nauta stain. The results from three animals are presented.

B. The results shown above have been summed to give an area represented by the hatched region. Superimposed upon this is a map of the cortical visual area from another animal. The band of degeneration from the three animals is seen to lie symmetrically about the VI/VII boundary and has a distribution similar to that of the binocular field projection (page 134).

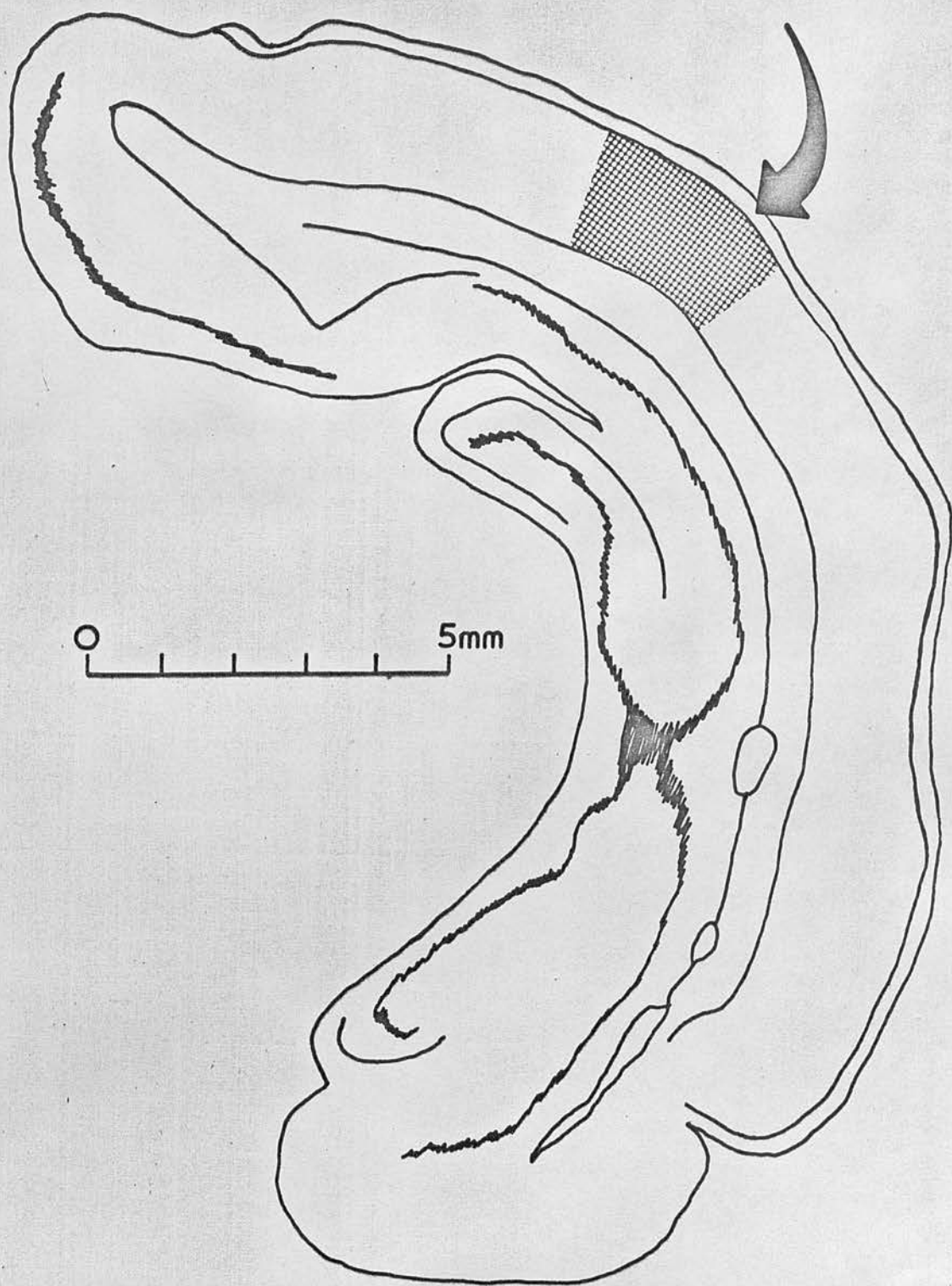


A



B

Fig. 93 Diagram of a coronal cortical section through the visual cortex. The hatched area indicates the distribution of Nauta stained degenerating fibres subsequent to the removal of the opposite hemisphere. The arrow indicates the position of the area 17/area occipitalis boundary judged from an adjacent Nissl stained section. When making the diagram, the Nauta material was enlarged to the dimensions of the Nissl section in order to compensate for shrinkage.



RELATION OF VI AND VII TO AREAS 17 AND OCCIPITALIS

INTRODUCTION

The maps of Rose (1931) and Rose and Malis (1965) show area 17 in the rabbit as being bounded medially by the splenial sulcus and caudally, in dorsal projection, by the posterior edge of the cortex. The anterior margin is about 12 mm. from the occipital pole and the lateral transition to the area occipitalis is placed some 12 mm. from the midline.

The above map of VI and VII shows a correspondence in its medial and posterior borders with the published cytoarchitectonic maps. The medio-lateral and anteroposterior dimensions of VI are, however, rather less than those of area 17 in the maps of Rose and Rose and Malis. Such a disagreement might be expected since the published work has been carried out on the generally larger American rabbits. Arden et al. (1967) have commented on this discrepancy between the published maps and the visual area of their experimental animals. In the rabbits used for the construction of the VI/VII map the anterior margin of VI lies about 10-11 mm. from the posterior pole of the cortex. The lateral margin lies from 9.5 to 11 mm. from the midline.

O'Leary and Bishop (1938) published 5 maps of the rabbit visual cortex which show the midline, splenial sulcus and both medial and lateral borders of the cytoarchitectonically determined transition zone from area 17 to the area occipitalis. There is considerable individual variation in the medio-lateral extent of area 17 but the correspondence of the medial border of the transition region and the lateral border of VI is excellent in two (fig. 8 and 11) cases, good in one and bad in two. This information supports the correspondence of the VI/VII junction, 17/occipitalis border and projection line of the transcallosal fibres that was suggested in the previous section. Only one experiment has been carried out to attempt confirmation.

METHODS

At the cessation of an experiment in which the cortex had not been penetrated by electrodes and was thus free of trauma, surface recordings were /

were made of the response to visual stimuli. The VI/VII border was located and a knife cut was made along a line corresponding to a meridian in the visual field some 10° temporal of the anterior limit of the field. The brain was processed in the usual fashion.

RESULTS

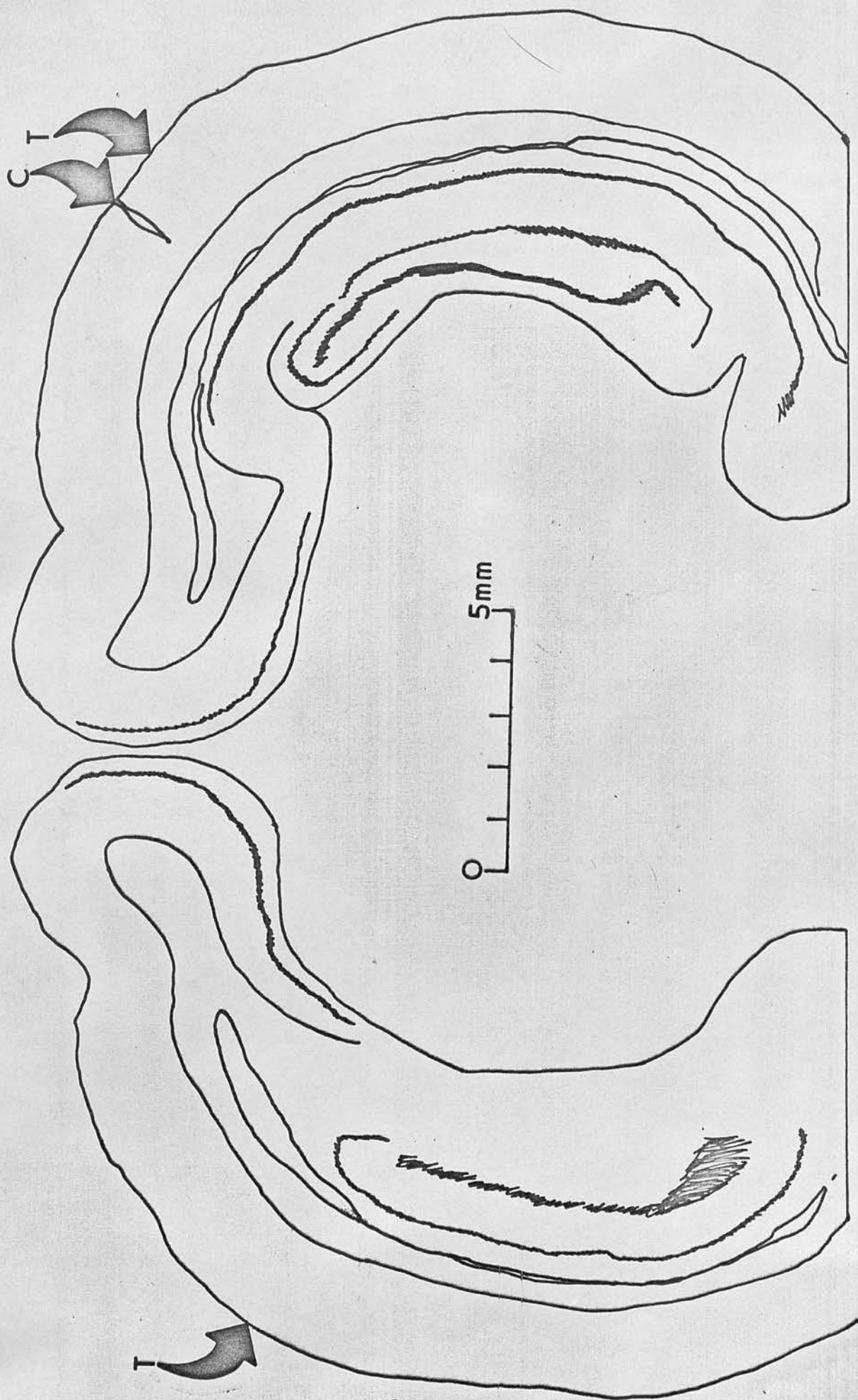
The lateral limit of area 17 was determined by microscopic observation in sections from both hemispheres and was found to correspond. The knife cut was observed to lie about 1 mm. medial of the border (fig. 94).

DISCUSSION

The results indicate that the transition zone from area 17 to the area occipitalis bears the projection of the VI/VII boundary. The area 17 thus corresponds quite well with VI. There is some difficulty in comparing the sharply defined VI/VII border or decussation line with the more vague cytoarchitectonic transition but the greater part of VII must project on to the clearly defined area occipitalis and only a portion on to the transition zone. The lateral border of VII has not yet been defined and it is not known whether a third representation of the visual field is present beyond that border.

Hubel and Wiesel (1965) claim to have shown the correspondence of area 17, 18 and 19 with VI, VII and VIII respectively in the cat. Comparison of the electrophysiologically determined map of the cat visual cortex (Bilge, Bingle, Seneviratne and Whitteridge, 1967) with the cytoarchitectonic map of Otsuka and Hassler (1962) confirms their claims. A similar correspondence of area 17 and VI has been established by Cowey (1964) for the spider monkey. A second, mirror image, representation of the visual field in the prestriate region was also described but histological controls were not described and it is not clear whether this corresponds to area 18, 19 or both.

Fig. 9a. Coronal cortical section in a plane of the visual cortex. The arrow C indicates a knife cut which was made 10° medial of the VI/VII boundary as determined electrophysiologically. The arrows at T indicate the position of the cytoarchitectonically determined boundary between the area 17 and the area occipitalis.



SINGLE UNITS OF THE VISUAL CORTEX

INTRODUCTION

Single unit recording from the rabbit visual cortex is not easy .
Two phenomena

1. burst discharge
2. 'switching off' of cortical activity

can play havoc with an attempt to systematically analyse the behaviour of a single unit.

The burst discharge is similar to that recorded in the rabbit LGN by Arden and Soderburg (1961). High frequency bursts of 3-4 spikes follow one another at a rate of about 3-5 per second. Quantitative descriptions of the spontaneous activity of single units in rabbit retina and LGN have been presented by Arden and Soderburg (1961); the activity of cortical units in unanaesthetised rabbits has been described by Velyka (1965). Creutzfeldt, Fuster, Herz and Straschill (1966) describe activity at all three stations of the visual pathway in rabbits anaesthetised with nembutal. The activity of retinal or optic tract units is found to be random. The spike interval histogram is unimodal and few intervals are greater than 50 m.s. The interval histograms of LGN and cortex show a considerably greater range of intervals than those for retina or optic tract. Joint interval histograms show that short intervals are more often followed by short and long by long. Such behaviour reflects the characteristic grouped discharge of the regions. Burst activity has not been recorded from the retina or optic nerve of rabbit or cat. Grouped firing in the LGN and cortex thus bears no relation to the cyclic activity which appears in the retina of the rat under barbiturate anaesthesia (Brown & Rojas, 1966).

At one time burst firing was thought to be a manifestation of abnormal conditions such as local injury or anaesthesia. The presence of such firing in the unanaesthetised or encephale isole animal suggests that this is not the case. Burst firing in the LGN of a conscious, unrestrained cat has been found to predominate in natural sleep but is abolished upon arousal even in complete darkness (Hubel, 1959). In the visual cortex of such a cat, arousal /

arousal is seen to be accompanied by a smoothing out of grouped firing and the onset of a random discharge.

Burst firing in the rabbit cortex was found in animals under nembutal, paraldehyde, urethane and ether anaesthesia. The phenomenon is not so marked in preparations kept lightly anaesthetised and ether anaesthesia was thus found to be the most satisfactory in view of the great facility with which the anaesthetic level may be controlled.

On many occasions a single unit which responds well to visual stimuli will quite suddenly become refractory for a period of up to three minutes and will then return to its normal sensitivity. A similar phenomenon has been described by Arden and Soderburg (1961) as occurring in the rabbit LGN. Such periods of cortical 'switch off' are a considerable hindrance to the study of unit behaviour but can be avoided by careful adjustment of the anaesthetic supply.

The best preparations show a very active upper cortex. A hissing sound is encountered on contacting the lamina zonalis, which receives projections from all of the underlying layers and is a good region to sample the overall activity level, while single units with small receptive fields are recorded just below. If the animal is too deeply anaesthetised, i.e. does not withdraw its paw in response to a hard squeeze, then the upper cortex is usually found to be non functional. This finding is in accord with that of Valleola (1961) who reports that units were sampled with equal frequency in the upper and lower claustrinsular cortex of lightly anaesthetised rabbits but that in deeply anaesthetised preparations the units were predominantly recorded from the lower layers.

METHODS

The preparation of the animal and exposure of the cortex were in accord with the account in the general methods section. As outlined previously, ether was chosen as anaesthetic. Tungsten and Wood's metal electrodes have been used with equal success in locating units. The best results /

results have been obtained during the period from 6 to 18 hours after the induction of anaesthesia. In the earlier experiments urethan was used as an anaesthetic with some success. The depth of single units was estimated by reference to the surface of the cortex, whose position was read at the beginning and end of the stab, and the transition from layer VI to the white matter. Stimuli were presented either by the methods described in the appendix or by an 'Airmark' perimeter.

RESULTS

Small receptive field units ($1-3^\circ$). These units were most commonly found in the upper half of the cortex. The fields are from $1-3^\circ$ in diameter when plotted with the 'Airmark' perimeter 10' spot and appear to be homogeneous in their response characteristics. The majority of the units possess on-off receptive fields although a few pure on or off types were encountered. An inhibitory surround could not be demonstrated by a light spot flashed on or off but the response to the movement of wide edges through the receptive field was less vigorous than that to small objects. The expanding spot test (p. 51) elicited a response from the surround of some of the units upon both expansion and contraction of the projected disc. The responses were quite rapidly adapting and their latency was in the order of 60 m.s. when a bright 1° light spot was flashed in the receptive field centre. Firing in response to the rapid movement of objects or shadows through the receptive field was not very good (fig. 95e). The waveform of the spikes was usually monophasic. Some responses of a typical unit are shown in fig. 95.

Medium field units ($5-10^\circ$). Another group of units with homogeneous on-off receptive fields was recorded but these possessed larger, $5-10^\circ$, fields and different properties to the small field type. The medium field units showed behaviour similar to the large field off units of the optic nerve. The units respond to the movement of small objects or shadows within the receptive field and fire in response to step like changes in the illumination level. Unlike the large field off fibres, of the optic nerve, they show a response /

response to both incremental brightening or decremental dimming. The response to such stimuli was very markedly reduced when the field and surround were illuminated together which suggests the presence of some arrangement for lateral inhibition (fig. 96c,d). The firing pattern of these units does not follow very rapid movement in the receptive field so faithfully as the optic nerve units but up to about 100°/sec. their response is good, (fig. 96e,f). Latencies were in the order of 60-70 m.s. Responses of some units of this kind are shown in fig. 96.

Directional units. Only one half of the population of recorded cortical directional units would respond with firing to a small spot of light flashed in their field. All of those units were of the on-off type and possessed fields from 3-7° in diameter. The response was much better to a moving card stimulus than to the moving bar projected by the visual stimulator. The preferred direction for motion remained the same in all cases under stimulus contrast reversal. The response could be elicited by the movement of a small object into the field over an arc of about 180° and thus appeared to differ from that of retinal directional units which fire to movements along radii subtending an arc of about 270°. Inability to cause firing of cortical units with the projected light bar from the stimulator prevented the collection of quantitative data for comparison with the results obtained from optic nerve units. The illustrations of fig. 97,98 show the response of a cortical directional unit to movement of card stimuli along different radii under normal and contrast reversed conditions. The preferred direction was almost always at right angles to or parallel to the visual streak but some units (20%) evinced other preferred directions. Lateral inhibition was manifested only when very wide edges were used as stimuli (30° or so). The response was reduced but not eliminated when such wide stimuli were used.

On-off adjacent units. The response of this class of units was rather variable but the most obvious feature was that they fired to the movement of edges in either direction along an axis passing through the centre of both /

both the on and the off regions of the receptive field. The on and off areas were spatially separated and homogenous in the form of their response to a light spot although in the region at which the areas bordered on one another it was possible to map a strip giving on and off responses. Some of the units have shown spontaneous activity in the light. In these cases, it was found that a black disc placed over the on region inhibited the spontaneous activity. If the room was then darkened, it was found that the spontaneous activity started up again. No firing could be obtained by moving an edge across the on and off fields simultaneously. It is clear that the two regions of the field possessed mutually inhibitory connections. The properties were thus similar to those of the retinal on-off adjacent units. Movement of a black edge into the off field caused firing until the on area was reached while movement back along the same axis elicited firing as the on field was uncovered. Bar stimuli produced more complex results when moving. A stationary bar flashed in the field would cause firing over a limited range of orientations. A one or two degree wide bar orientated across the middle of the field and set at right angles to the axis joining the centre of the on and off regions caused marked firing when flashed on and off. A rotation of the bar by 25° either way considerably reduced the response. Edges orientated at an angle of more than 30° to their direction of motion along the major axis of the field would rarely cause a good response. The major axis of the field (through on and off field centres) was usually from $6-12^\circ$ long. The minor axis was about $4-6^\circ$. Elliptical fields are the most common although circular types are found. The movement sensitive axis of these units was usually found to be at right angles or parallel to the visual streak projection.

Three units were obtained with more sophisticated requirements. They fired spontaneously and were very difficult to locate. The adequate stimulus was finally found to be a narrow bar or thin wire (1 mm.) passed across the field at a certain orientation. A single edge would not cause firing so that it would appear that a lateral inhibitory field must be present on each side /

side of the excitatory area. A slight change in the orientation of the wire eliminated the response. One of the fields responded to motion of the bar in one direction only, the others responded to back and forth movement. A response could be obtained to movement along radii subtending an arc of about 30° .

Some of the behaviour of the common on-off adjacent field is shown in the figs. 99

Very large field units ($20-40^\circ$). It is possible to record single units with very large receptive fields in the region extending from 0.75 mm. to 1.5 mm. below the cortical surface. These units are often present, firing spontaneously, in preparations whose upper cortex is not at all responsive. The action potentials are often of great amplitude and complex waveform. Some lesions have been made when recording from such units and subsequent histological examination showed the electrode tip to have been present in layers V or VI. These fields were often the last form recorded before entering the subadjacent white matter. The majority of the units showed a homogenous on-off field but a few pure on types were recorded. The fields were very sensitive to small movements of stimuli or shadows. Many more spikes were obtained in the response to moving stimuli than in that to an on-off light spot flash. These units are quite unlike anything recorded from the optic nerve.

Unidentified fields. Seventeen units have been held for an adequate length of time for routine analysis and identification without classification having been made successfully. In some of these cases only the spontaneous activity revealed the presence of the unit and responses to visual stimuli were absent. These units may not be dismissed as non visual for their behaviour is similar to that of the more sophisticated orientation sensitive units before the receptive field is located. In other cases it was possible to obtain responses to visual stimuli but no specific spatially located field was observed. It is thus likely that units performing more complex functions are present but their functions have not been identified.

Depth /

Depth of various unit classes. Figure 100 shows depth histograms for single units with the various classes of receptive field described above. The total sample used for the construction of the graphs included 116 units. The number of each of the classes was similar. The laminae of the cyto-architectonic analysis are included as a rough guide. Units are listed as being recorded from the cerebral cortex but it is possible that many of the units are of extracortical origin and represent geniculate fibres spreading up into layers four and three. No systematic analysis of the units into cells and fibres was achieved although all spikes were examined on a high speed time base.

The clearest differentiation is between the group of upper layer units and the population of large field units which seem to predominate in layers V and VI. These very large field units are presumably of cortical origin and may be able to be identified with the large pyramidal cells of the region.

VIII Number of cortical units recorded in each category.

Type	No.	%
Small receptive field	47	25
Medium receptive field	33	18
Directional units	37	20
On-off adjacent	30	16
Very large field	39	21
Total	186	100

The above percentages cannot be taken as indicating anything significant about cortical function as they must undoubtedly reflect very considerable sampling errors resulting from the equipment used, anaesthetic level, etc. One point worthy of note is that units with relatively sophisticated behaviour i.e. directional and on-off adjacent units made up 36% of the total recorded sample in the cortex but only 11% in the optic nerve in spite of the fact that they form a large percentage of retinal streak units. It would appear that some effect other than the analytic procedure used for identification /

identification of unit types accounts for the lower percentage of such units in the optic nerve. The suggestion of page 59 may be valid.

DISCUSSION

Comparison of results with literature on rabbit visual cortex units.

At the time when these results were in preliminary form (Hughes, 1966) there had been no detailed analysis of the units in the rabbit visual cortex. The paper of Lomo and Mollica (1962) reports on sensory interaction in the visual cortex of this animal but the units were subjected to an examination with flashed diffuse light stimuli. Similar stimulating methods were used by Velyka (1965) who uses the Jung classification in terms of on-off responsiveness for the units recorded.

Recently Arden, Ikeda and Hill (1967) published a description of cortical units which is essentially in agreement with that given above. Directional, on-off adjacent and very large field units are described under different titles although it is not clear whether a population of on-off directional units was recorded. The on-off adjacent units are described as rare although in this series of experiments they were as common as most of the other types. The fields of the units recorded by Arden et al. appear to be much larger than some of those described above. No mention is made of the small field on-off units which formed the largest single class of the above sample. The majority of the units shown appear to be the very large field type. Arden describes these units as possessing a region within the field which is especially sensitive to movement and may lie at the centre or periphery of the receptive field. Such a feature was not observed in the above experiments but, as yet, the opportunity to attempt confirmation of Arden's finding has not arisen. Arden et al. studied 36 units whose waveforms were routinely monitored. These are described as cells although no criteria used in the identification are stated.

It appears likely that Arden's group have recorded predominantly from the units of the deeper cortex which possess the large fields he describes

(40-50° in diameter). It remains to be seen whether the large population of units with smaller receptive fields which have been recorded from the upper cortex in this series are cells or fibres coming into the cortex from the LGN. In view of Walls' finding (1965) that dendrites conduct spikes it may be difficult to determine whether single units recorded in the upper layers are LGN fibres or post-synaptic elements.

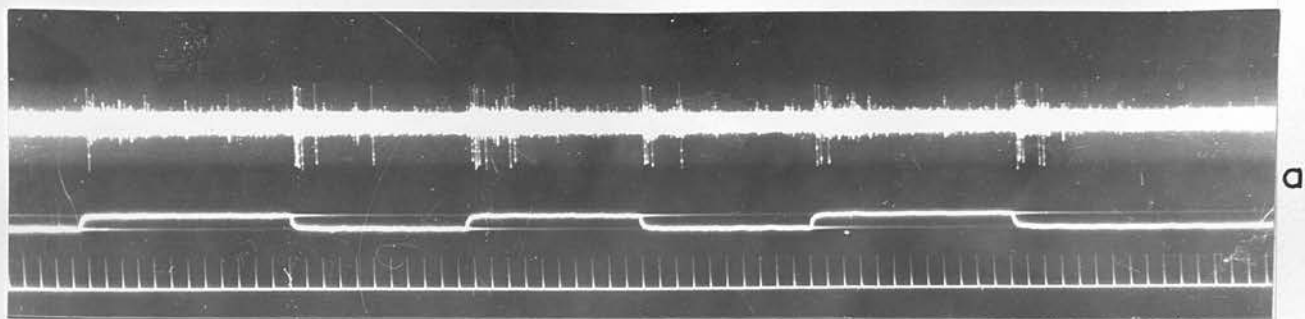
Small field cortical unit responding to the flashing of a 1° spot centred on its receptive field . In this and subsequent photographs on this page the upward movement of the monitor trace indicates dimming of cessation of illumination.

The response is enhanced when a 3° spot is flashed in the receptive field centre.

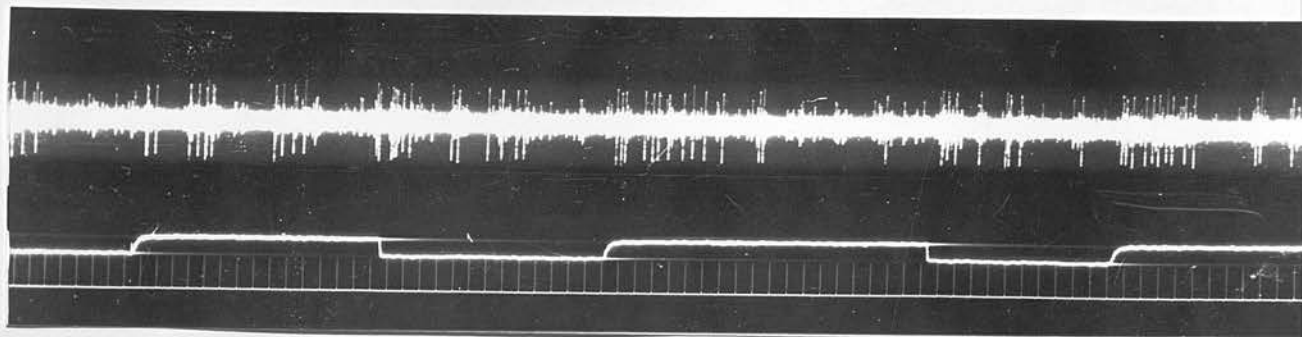
Flashing of whole field illumination reduces the response indicating the presence of a lateral inhibitory surround.

Somewhat inconsistent responses are given to incremental and decremental intensity change .

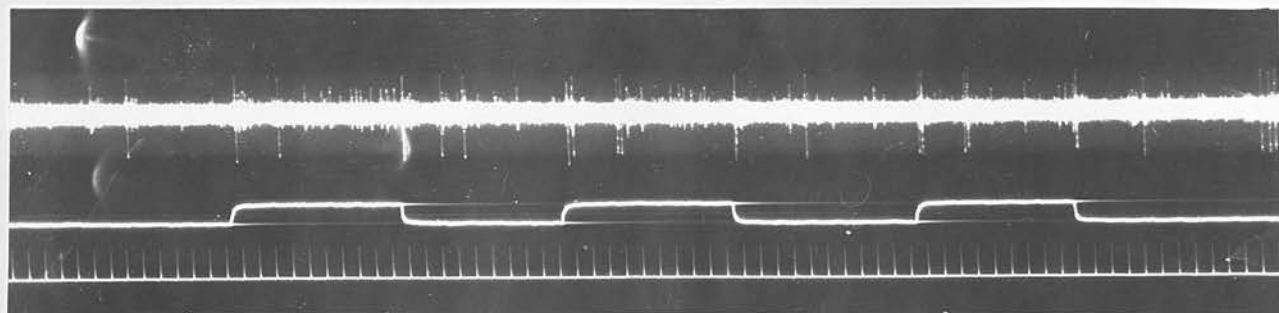
Response of the unit to the rapid passage of a 1° black card disc through the receptive field at various velocities. The unit gives a single spike to rapid movement , photocell response on monitor trace has narrow peak , and a short burst to slower moving stimuli , photocell record shows wide peak .



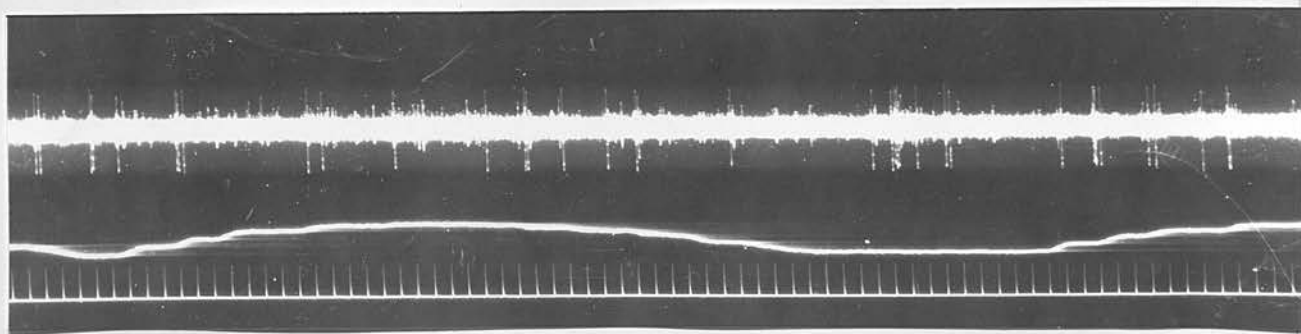
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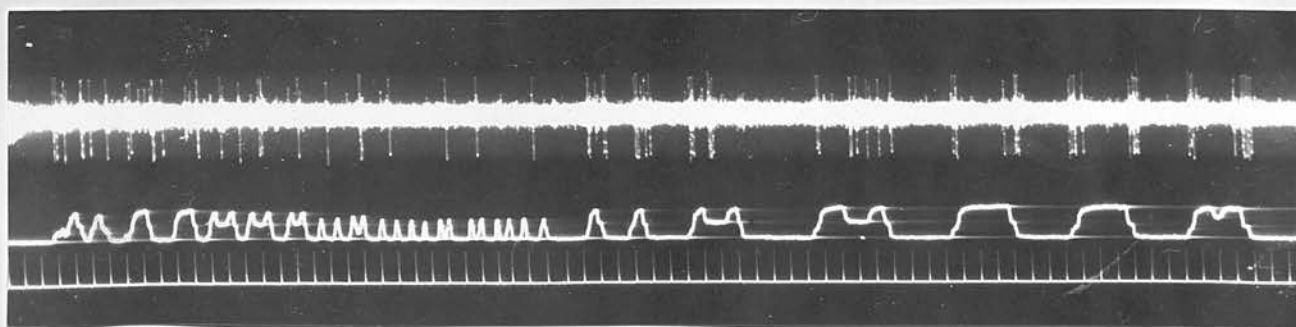
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d



e

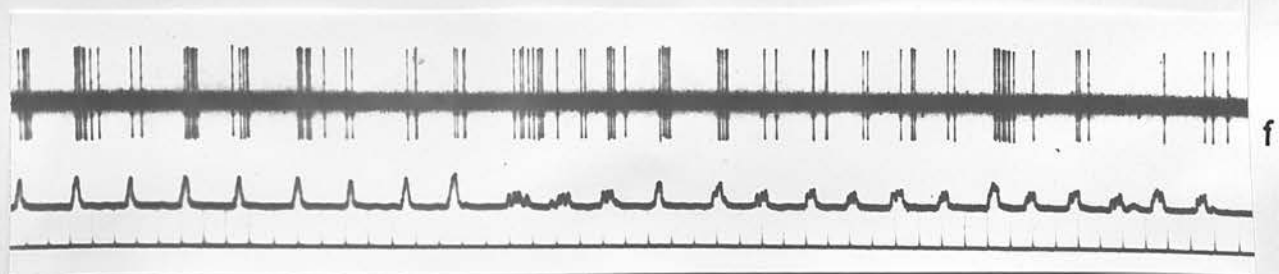
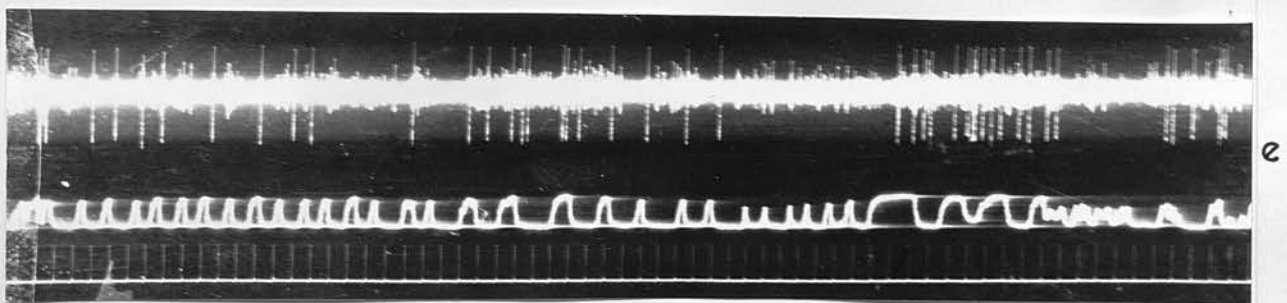
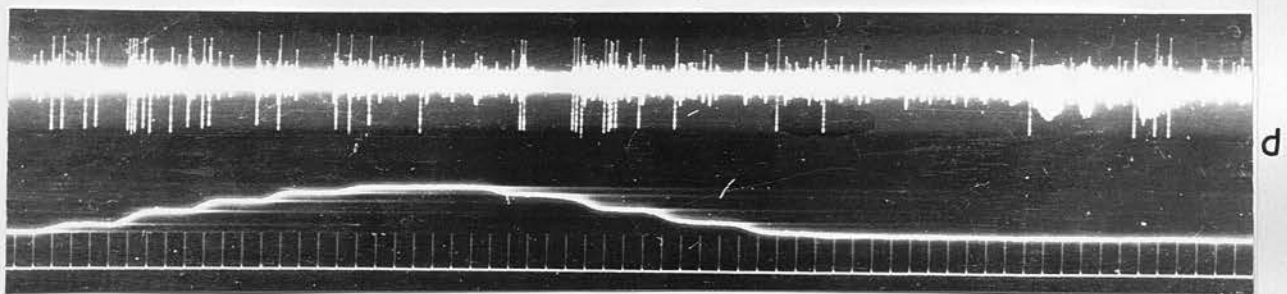
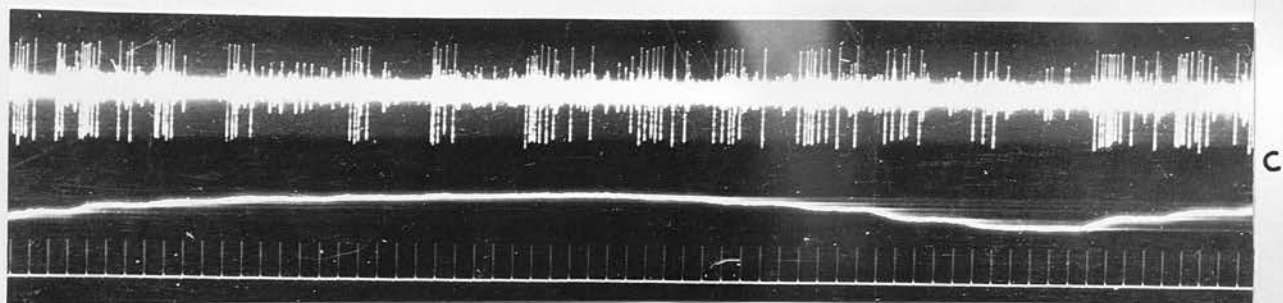
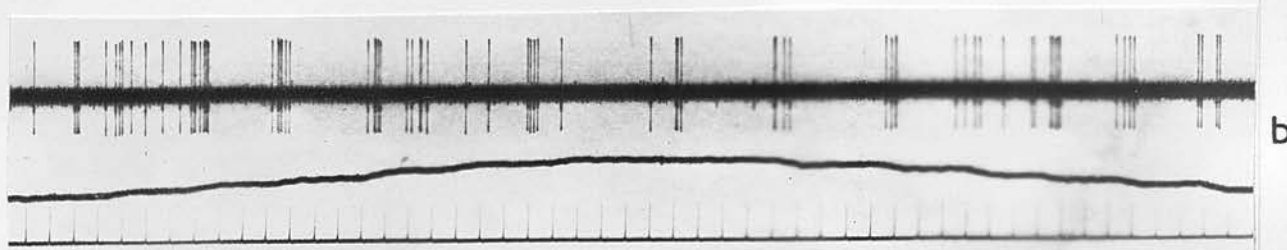
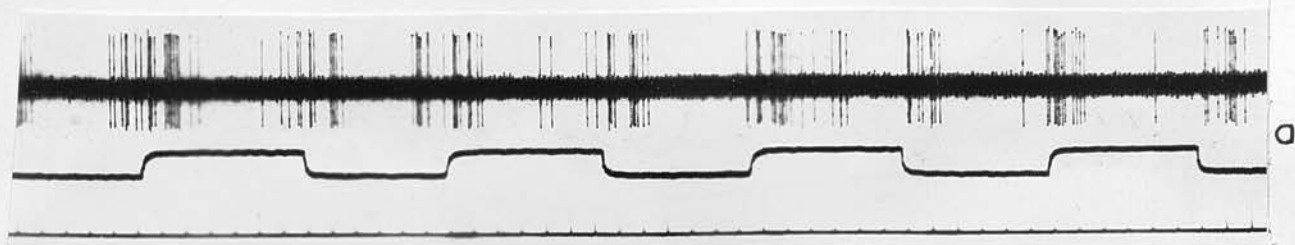
Medium field cortical unit. Response to on and off of a 3° light spot flashed in the receptive field centre. In this and subsequent photographs on this page the upward movement of the monitor trace indicates off or dimming of the light source.

Response to decremental dimming and incremental brightening with 3° spot of illumination centred on the receptive field.

Another record similar to the previous case .

Step changes in illumination , as above , but with whole field illumination . The response is considerably less clear .

e & f. two examples of medium field units responding to the rapid movement of a card disc stimulus. The second unit responds well .



Directional unit. Response to flashing of a 3° spot centred in its receptive field. Off of the light is indicated at the upstroke of the monitor trace .

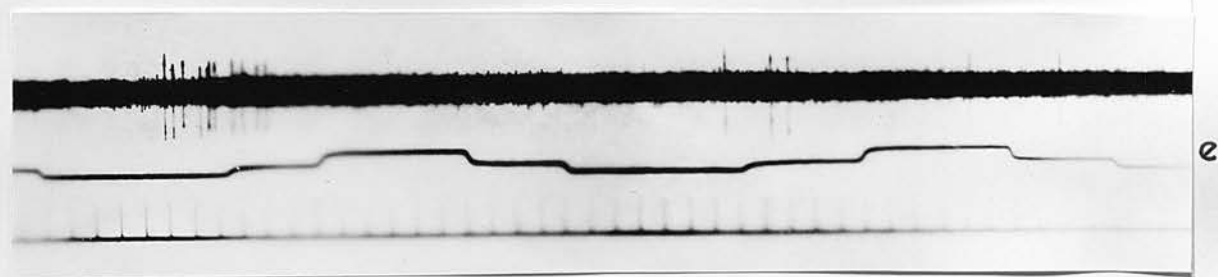
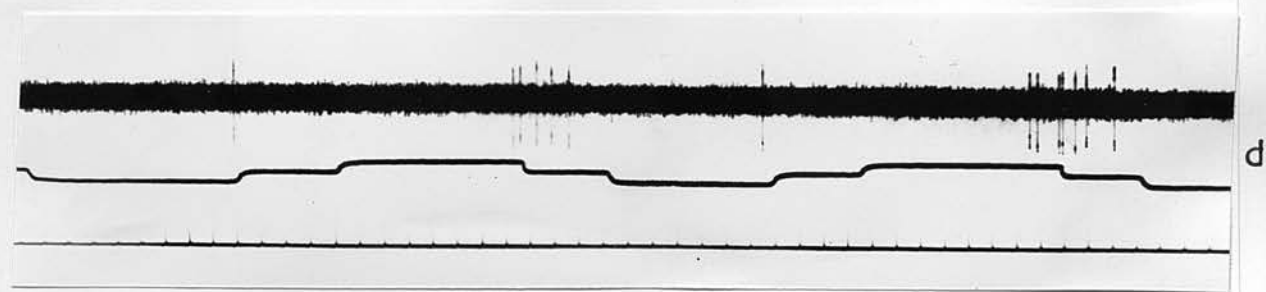
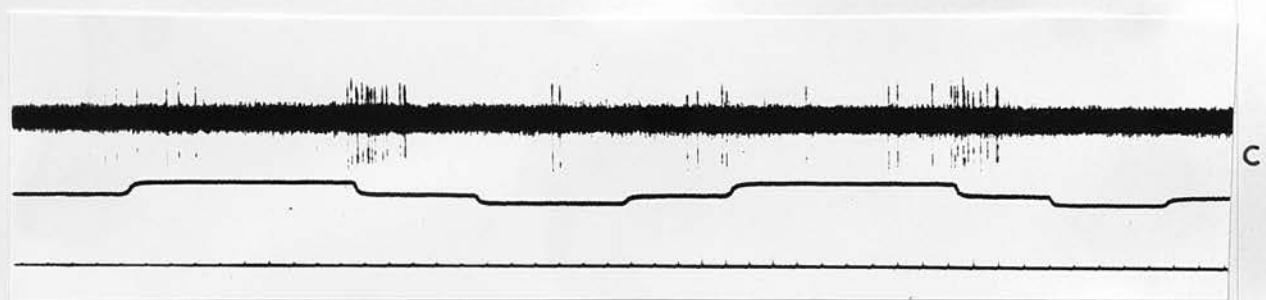
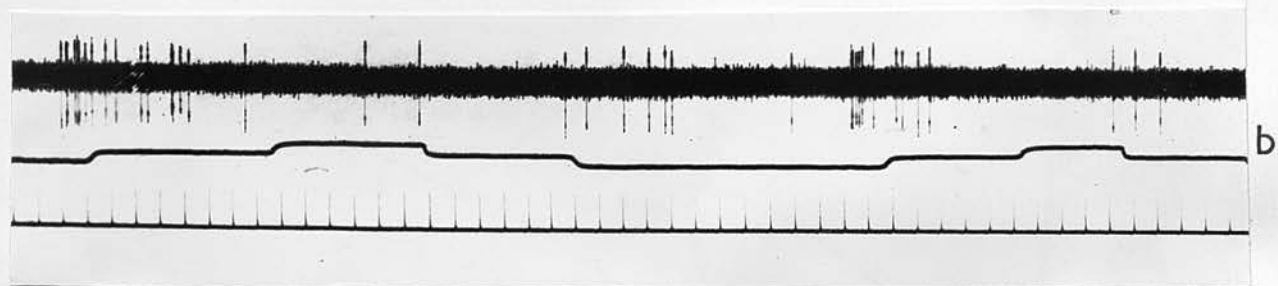
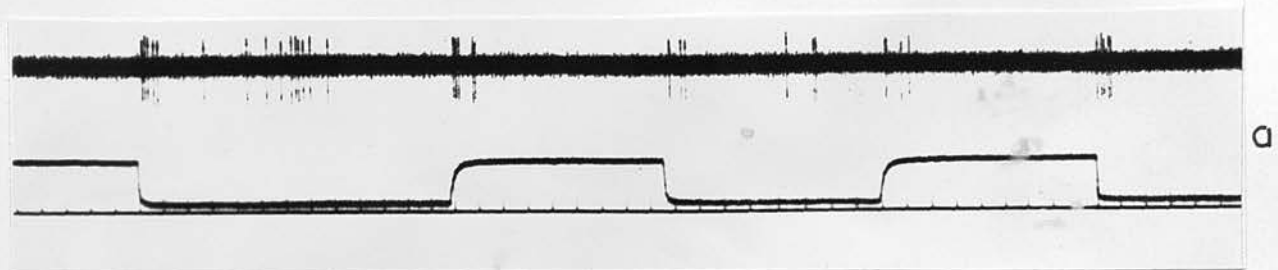
b,c,d,e, the first step in the monitor trace shows entry of an edge into the receptive field . The second step shows the exit of the edge- return steps indicate movement in the opposite direction . Edge is black on a white background.

b, -up-down.

c, down-up.

d, temporal-nasal.

e, nasal-temporal.



Continuation of the responses of the directional unit above. In this case , however , the stimulus contrast has been reversed and the edge is white on a black background . The new contrast is less effective as a stimulus but the firing remains directional . Monitor strace as above .
a, up-down.

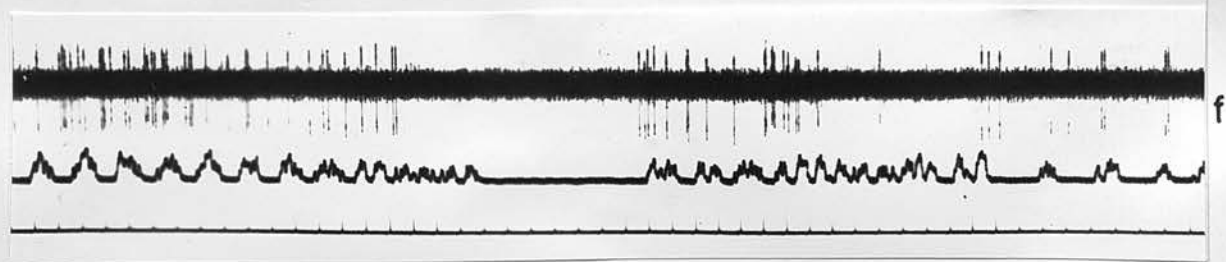
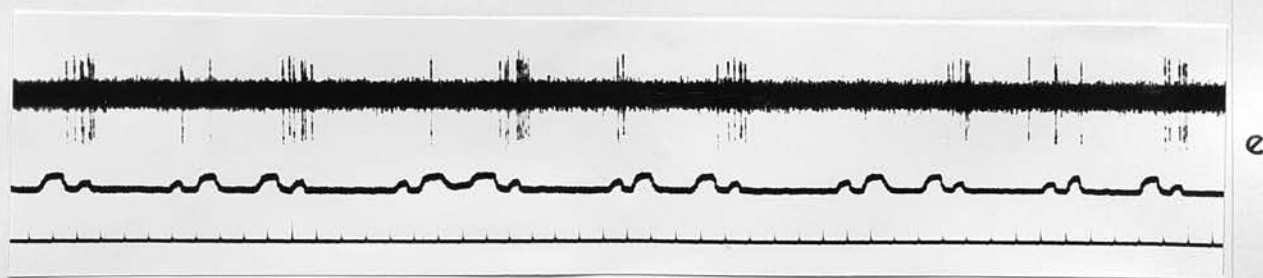
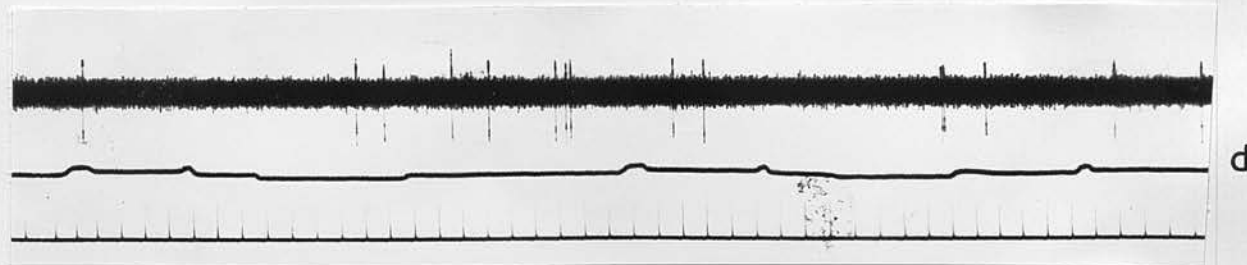
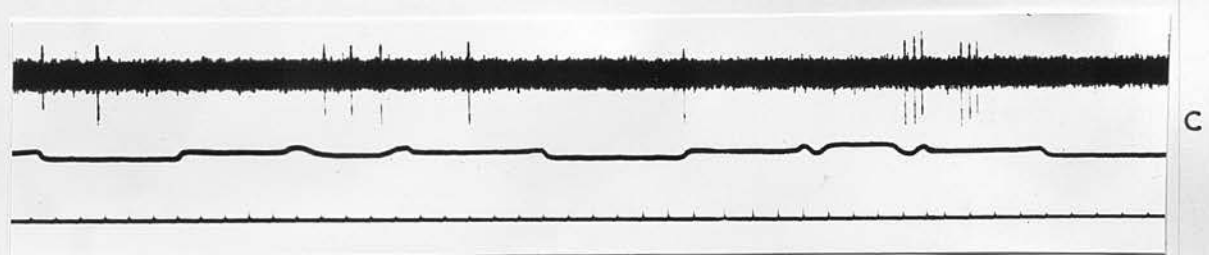
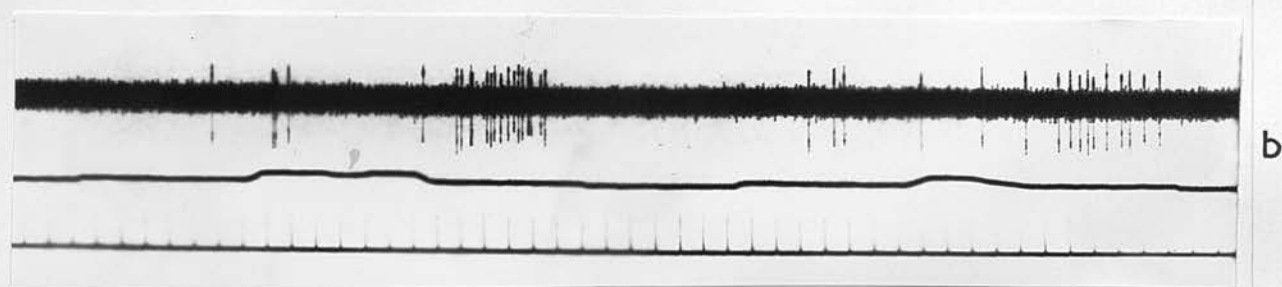
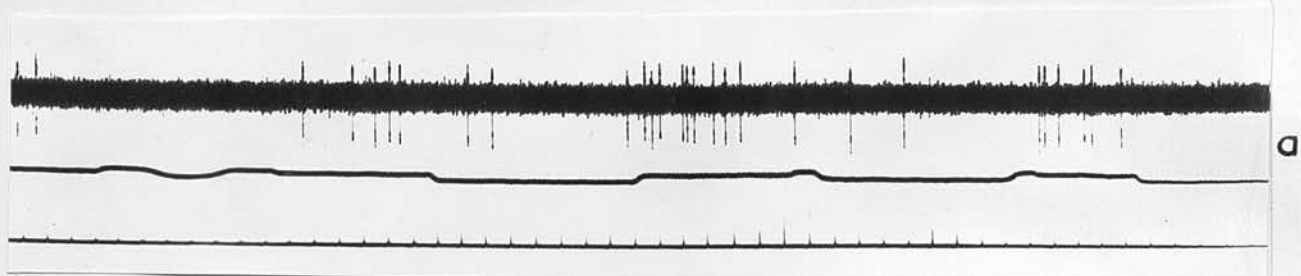
b, down-up.

c, temporal-nasal,

d, nasal-temporal.

The response of the unit remains directional even to down-up movement of the edge at 100/sec. Photocell output on monitor trace monitors entry and exit of the stimulus.

The directional unit still responds to stimulus velocities in excess of 300°/sec .



Orientation unit of the cortex . A 1° wide by 5° long white bar on a black background is flashed on the receptive field in an orientation twisted 25° from the optimum vertical position . Cessation of illumination is indicated by the downward movement of the monitor trace . The firing of the unit is poor.

The bar is flashed in its optimum vertical position . The response is good. The photograph should in this case be read from ~~right to left~~ because it has unfortunately been printed in reverse.

A 25° twist of the stimulus orientation in the opposite direction reduces the response considerably .

The following series shows the response of the same unit to a moving 5° by 1° white bar passing across the receptive field from nasal to temporal in various orientations . The monitor trace rising phase indicates the position of the stimulus in the visual field. The period during which the stimulus passes through the receptive field centre is marked by small bumps on the trace which were produced by photocells placed on each side of the field. First picture shows response with stimulus 25° twisted from optimum orientation .

Stimulus in optimum orientation .

Stimulus twisted 25° in opposite direction from optimum orientation .

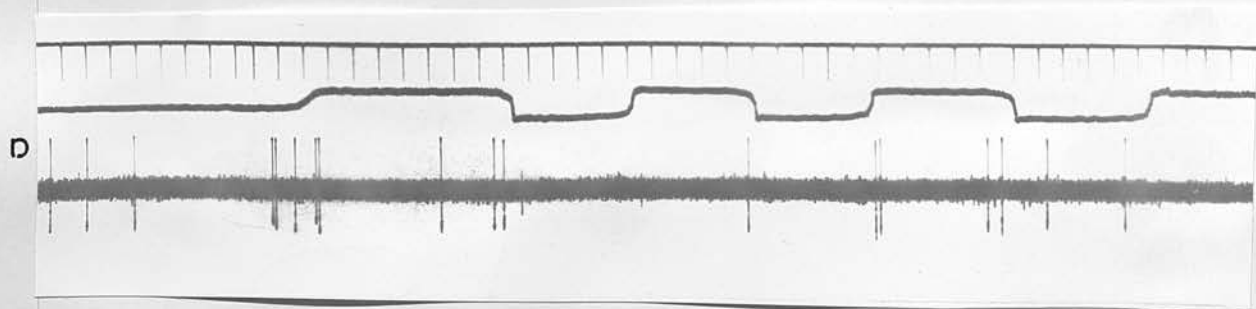
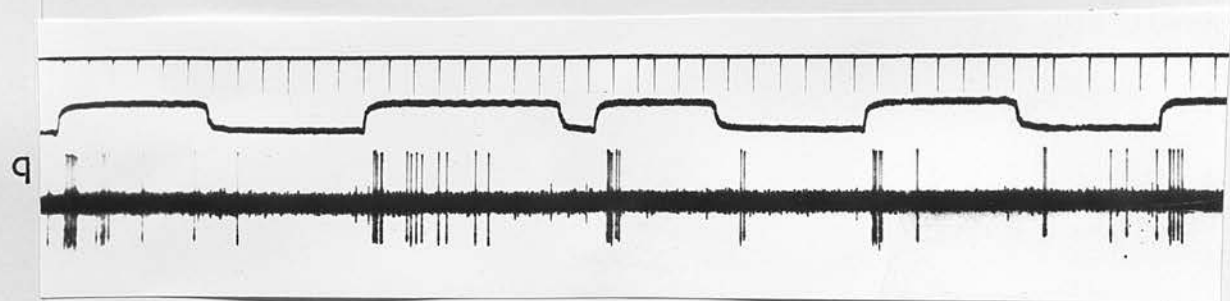
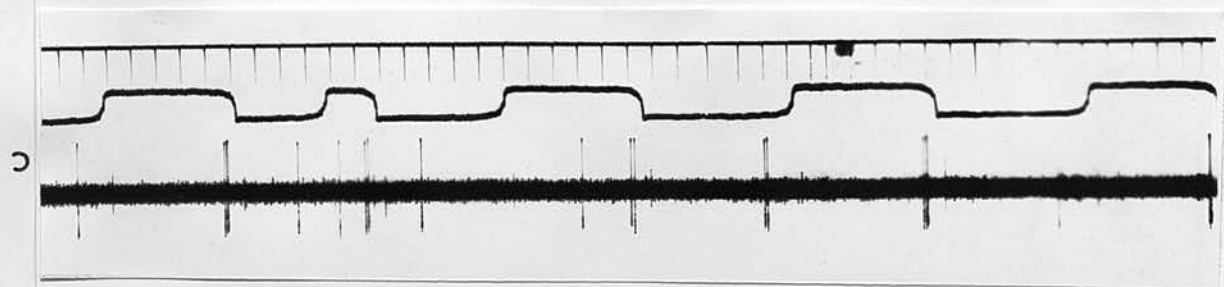
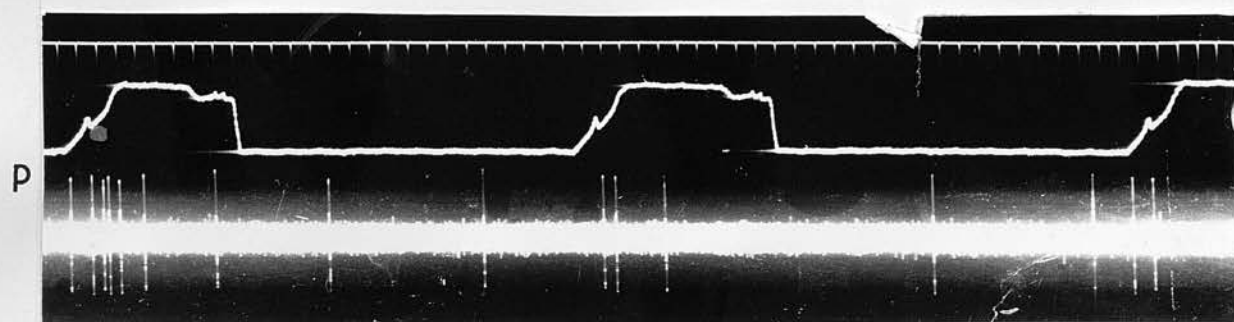
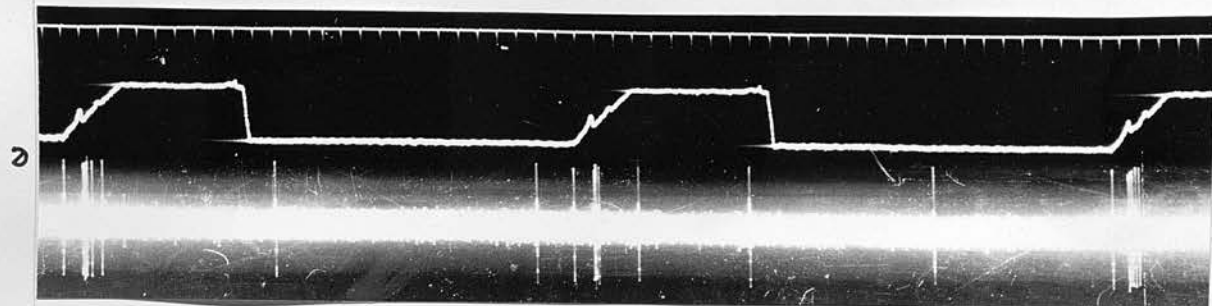
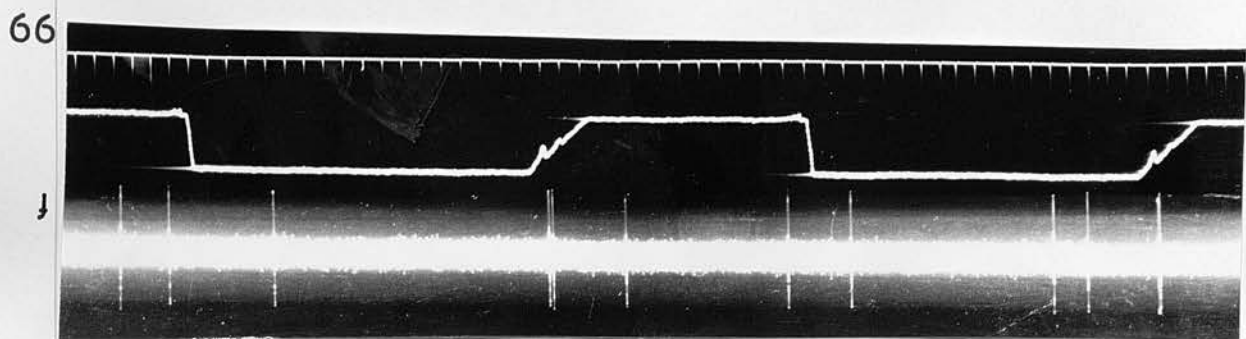
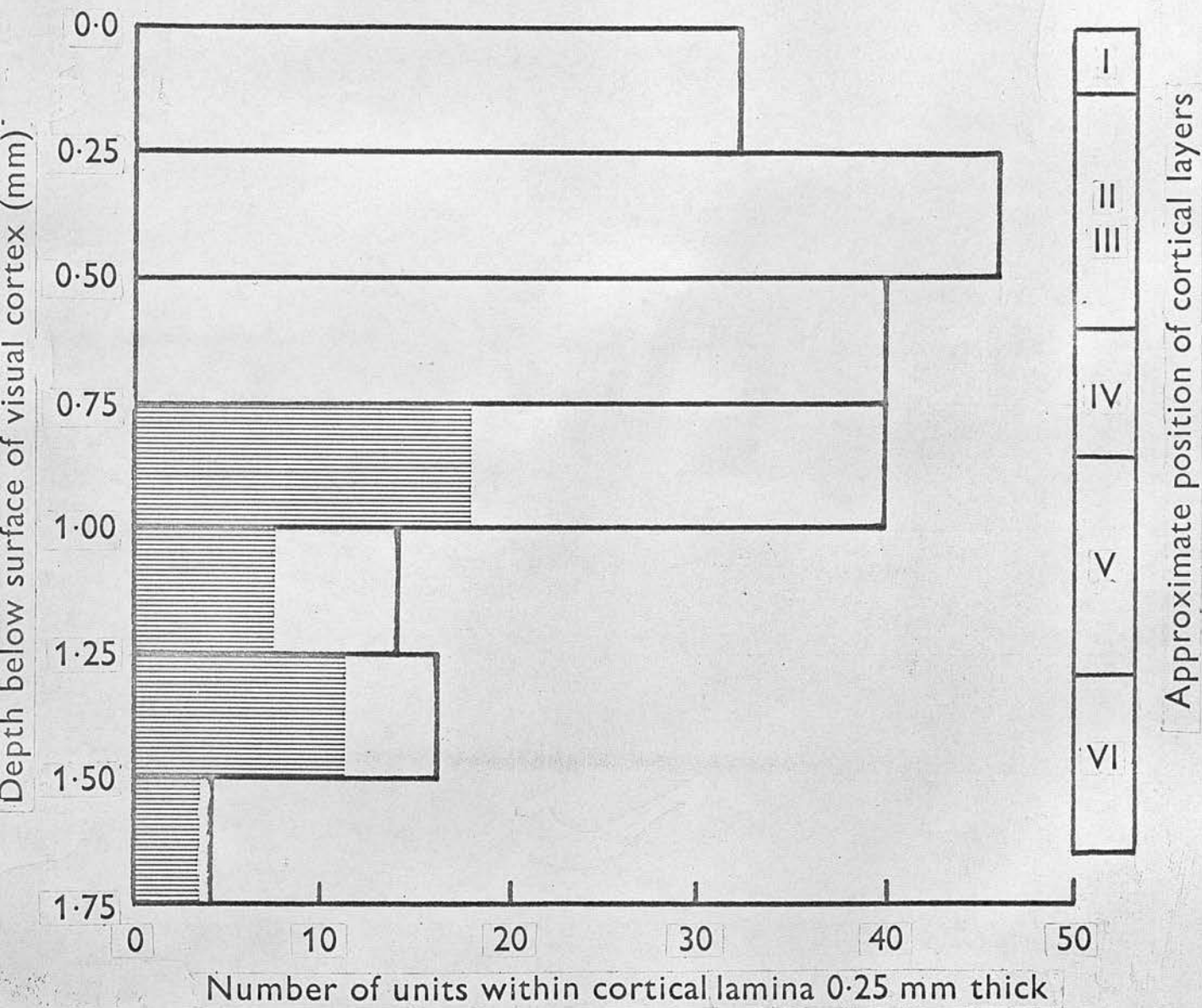


Fig.100. Depth histogram showing the number of single units recorded within 0.25 mm. thick cortical laminae. The hatched columns indicates the number of very large field units. Other classes of unit are lumped together for they show similar distributions.



RABBIT EYE MOVEMENTS

In extreme alertness when the retractor bulbi is relaxed, ~~the~~ the rabbit eye protrudes for up to 1 cm. beyond the rim of the orbit so that, aided by several other adaptations, its field of view is relatively unobstructed and the animal possesses the enormous visual field indicated in fig. 3 . When a rabbit is startled it 'freezes'. All body and eye movements are inhibited but, because of the extensive field of view, the animal will receive some indication of events in almost every region of the visual space around it without carrying out those eye and head movements which the visual system of predators is often so well adapted to detect. Such continued tracking of potentially dangerous visual stimuli during the freeze response is an important aspect of rabbit behaviour because of its reliance upon running away as a means of defence. Walls (1942) comments that animals with markedly lateral eyes are commonly noted for their defencelessness. The optic axes of the rabbit are almost set in a straight line. Reports in the literature on the angle between the optic axes vary from 155° to 170° (Sheppard, 1961).

A great amount of sclera is displayed when the rabbit is frightened. According to Walls (1942) this may be taken as indicative of considerable eye mobility. In contrast, however, several early workers were able to detect only vestibular reflex eye movements and neither spontaneous nor visual reflex eye movements were observed in the rabbit (Bartels, 1931; Urbantschitsch, 1910).

The situation was resolved when Brecher (1936) and Ter Braak (1936) independently discovered that rabbits 'freeze' and inhibit eye movements when placed inside the small rotating drums which are normally used to induce OKN. Field holding reflex nystagmus was readily induced when Brecher placed rabbits in a large rotating drum 1.3 m. in diameter and 1.6 m. high. 'Stare' or field holding nystagmus could be elicited in the dark by movements of a single light (Ter Braak, 1948) but if the illumination of the background was increased sufficiently for stationary objects to become visible then the nystagmus ceased.

Neither /

Neither Ter Braak (1936; 1948) nor Brecher (1936) were able to induce 'look' nystagmus in which a single object is tracked across a visible but stationary background when rabbits were used as subjects. Food, lightspots and limited striped bands failed as stimuli. 'Look' nystagmus is, however, readily obtained in cats, dogs, monkeys and man.

The absence of 'look' nystagmus in rabbits is said, even in current literature, to be a consequence of the absence of an area centralis in the rabbit retina (Brecher, 1936; Ter Braak, 1936; 1948; 1962; Walls, 1942; 1962). The retina was assumed to be equipotential so that fixation would be of no value when tracking moving objects. Evidence for the presence of an area centralis, the visual streak, in the rabbit retina has, however, existed for some 50 years. The topography of the streak was first outlined by Kerr and Seneviratne (1963) while the present work contains a more detailed account.

The ganglion cell distribution maps described earlier clearly show the uniformity of ganglion cell count along almost the entire length of the projection of any visual field parallel on to the retina. Along this axis the equipotentiality of the retina creates a situation equivalent to that assumed by the early workers because, as in the case of an animal without an area centralis, no benefit would accrue from voluntary tracking movements along the horizontal. Along the projection of the meridia, however, the ganglion cells are most certainly not distributed in the uniform fashion assumed by Brecher and Ter Braak. The vertical ganglion cell distribution graphs (figs. 30) clearly show the limited region of retina bearing the peak counts over about 1,500 g.cell./mm².

The centre of the optic nerve head has been found to lie 3 mm., on average, above the line of highest ganglion cell density in the retina. The finding, from the section on the schematic eye, that 0.167 mm. on the retina is equivalent to 1° on the retinal visual field projection thus enables it to be established that the projection of the parallels which run through the middle of the optic nerve head and along the peak count of the streak will lie /

lie 18° apart in the visual field. In similar fashion the angular separation of the projections of the ganglion cell density map isocount lines may be determined. Fig. 101 shows such a projection of visual field parallels on to the squash mount retina RR7 (fig. 27). In this case the peak count region of the streak is used as a reference line.

It is not possible to see the visual streak in the conscious rabbit when examining the eye with an ophthalmoscope but the optic nerve head may readily be seen. Measurements made with the hand perimeter indicate the optic disc to have an elevation of about $20-25^\circ$ above the horizontal. The estimated 18° separation between the optic disc and the peak isocount line indicates that, when the eye is in the normal position, the middle of the visual streak receives the projection of a parallel within a few degrees of that which would intersect the horizon were the animal to be seated on an infinite plane surface. It cannot be said that the visual streak receives the projection of the equator of the rabbit's visual field for the eye is tilted somewhat (p. 2) and the equator projects on to the retina about 15° below the streak. Allowance for inevitable shrinkage in the histological preparations would allow an even better agreement to be shown between the elevation of the optic disc and the angular separation on the retina between it and the visual streak.

If the narrow region of streak bearing the peak ganglion cell count ($1-2^\circ$ wide) is used by the rabbit in a manner similar to animals with a circular area centralis, then it might be expected that tracking and 'look' nystagmus should be able to be induced in the vertical plane in order that any stimulus of interest to the animal may be followed and examined in detail if it tends to move off the visual streak. It appeared possible that vertical tracking movements had not been reported in the literature simply because nobody had thought of seeking a differential response between stimuli moved along the vertical and horizontal. Some experiments were conducted using electromyography to detect eye movements in the vertical plane. Field stabilising OKN was observed in this plane when the animal was placed inside
a /

a rotating striped drum whose axis was horizontal but various stimuli of small dimensions failed to induce following.

Even if vertical 'look' mystagmus proves to be absent, then the cells of the visual streak, which have been shown to possess more sophisticated properties than those of the remainder of the retina (Levick, 1967), are not doomed to analyse those stimuli which come randomly, as a result of the animal's movements, to be projected on to the area centralis.

Ophthalmoscopic examination of the rabbit eye reveals that the myelinated band, which runs out from the optic nerve head, is always held horizontal if the animal is unanaesthetised and sitting upright. The visual streak runs for its whole length, about 170° , parallel to the band of myelinated fibres. Thus, since the middle of the streak receives the projection of the horizon, then the horizontal streak will receive the projection of the horizon along its whole length when the eye is in its normal resting position or when the animal is displaying the 'freeze' reaction. It may be that visual phenomena of the not very distant horizon of the rabbit are of such importance to the animal as to justify the existence of an area centralis which is used for the analysis of this region alone. Vertical tracking may simply not occur. It will be clear that the use of the area centralis in this fashion would necessitate an efficient stabilising system for the eye if the lateral extensions of the streak are to convey anything more than the wild swinging of the visual field at the animal's every move. The remarkable powers possessed by the rabbit in this respect were discovered some years ago during the course of investigations which were given a great deal of attention in Magnus's "Körperstellung".

In one series of experiments de Kleijn (1921) was able to demonstrate that the horizontal sagittal axis, and consequently the visual streak, of the rabbit eye remain at right angles to the vertical when head movements occur ranging from depression of the long axis of the head some 90° below the horizontal to raising it 10° above.

If it is borne in mind that the rabbit normally sits with its nose lowered /

lowered some 35° below the horizontal, then it will be clear that in daily life the head may take up positions in the vertical plane with the nose from 55° down to 45° up without any alteration occurring in the orientation of the visual streak with respect to gravity.

In a later paper, de Kleijn (1922), demonstrated the extent of rabbit eye stabilisation in other planes. It was found that the head could be rotated about an occipitofrontal axis by about 21° in each direction and in a horizontal plane by 17° each way without the alteration of the orientation of the eye in space. In many cases compensation was perfect beyond these limits. The constancy of eye position in the rabbit is not to be attributed to the labyrinthine reflexes alone for total compensation for head movements over the ranges indicated above only occurs if the neck reflexes are intact.

Magnus (1924) has demonstrated the ability of the rabbit to maintain its head in a constant orientation in space in spite of variations in body position. Blind or sighted normal and thalamic rabbits are indistinguishable by head posture when their bodies are placed in similar orientations. Destruction of both labyrinths in blind thalamic or intact forebrain animals results in a permanent loss of head, and eye, stabilisation. Animals which have been subjected to such experiments are shown, after Magnus, in fig. 102. The arrangement for head and eye stabilisation provides a very good example of the servo-system which has been likened to the stable platform of the battleship fire control (Whitteridge, 1960).

The higher animals, especially man, appear to possess mechanisms which transfer the retino-centric visual image to a spacio-centric form. The evidence for this phenomenon, involving vestibulo-visual interaction, is good (Gibson & Mowrer, 1938) although the region in which, and the mechanisms whereby, this transformation occurs are obscure. In part this results from a lack of information about the single units of the vestibular system and their projection. It is only comparatively recently that the cortical projection of vestibular afferents has come to be accepted (Kempinsky, 1951). Some evidence for the interaction of visual and vestibular inputs in the cat cortex /

cortex has been put forward by Kornhuber and da Fonseca (1962) but the stimuli applied to the labyrinth were galvanic currents while diffuse light was used to activate the visual system. Little can be expected from such attempts to bludgeon information from the nervous system.

The stable platform of the rabbit retina, the horizon scanning visual streak and the apparent absence of eye movements other than those required to stabilise the visual field show that the rabbit retina bears a much more constant relationship to the visual field coordinates than is the case in, say, cat, monkey or man. The parallels of the visual field coordinate system would appear to project to a constant level on the rabbit retina and the most frequent changes in the visual field projection occur only when the animal rotates to bring new meridia into position. Thus, in the rabbit, there does not appear to be so great a need for internal transformation of the retinally orientated image as in the higher mammals since the spatial orientation is already conferred upon the image by the head and eye stabilising system. The demands made upon the rabbit visual analyser cannot be as rigorous as those of the cat or monkey. In this respect the rabbit appears to be similar to the octopus.

Wells (1960) has shown that if an octopus is trained to recognise a horizontal and a vertical rectangle and to discriminate between them, then the ability is lost after the removal of the statocysts. After the operation the eyes of the octopus show no compensatory movements with respect to gravity and thus their orientation varies with the position of the animal's head. If the eye is at right angles to its normal position, then the trained responses are actually inverted. The animal cannot take cues from its environment to establish the vertical axis in the absence of its statocysts.

The extent to which the rabbit is dependent upon its fixed eye orientation for the analysis of the retinal image is not known. A perusal of "Körperstellung" reveals, however, a very significant difference between the cat, dog and rabbit. A hooded, bilaterally labyrinthectomised dog or cat will make no attempt to recover its normal posture if held upside down. If the /

the hood is removed, then the animal will invert its position. Neither hooded nor unhooded bilaterally labyrinthectomised sighted rabbits with intact forebrains will make an attempt to right their posture. Sketches of these animals, after Magnus, are shown in fig. 102. It appears that the rabbit, like octopus but unlike dog or cat, lacks visual space reflexes which would enable it to orientate its body from visual cues alone.

A natural question arises from the above account, "what happens to the position of a rabbit eye when the animal is on a slope?" It can be seen from fig. 103 that if the animal is on a horizontal plane then the important parts of the visual field near the ground are covered by retina bearing a ganglion cell count of at least 1,000 g.cell/mm². The high density region scans point at the same height as the rabbit's own eye. Some vertical tracking appears to be carried out under these circumstances by upward and downward movements of the head. On a slope, however, part of the streak receives an image of the nearby upper slope while, on the other side, the eye gazes into space. In this case detailed examination of events on the upper or lower slopes cannot be achieved by head movement alone. It is necessary that the labyrinthine control of the eye orientation in space be overcome in some way so as to arrange the image of the appropriate region of the visual field on the streak unless the greater part of the extensive area centralis is to be rendered ineffective under these conditions.

Brecher (1936) has shown that the experiments of Fleisch (1922) which suggested that the rabbit might use voluntary eye movements were interpreted erroneously. The total visual space of Fleisch's animals consisted of one small light spot in otherwise dark surroundings. As was described previously, under these conditions the field fixation reflexes ensure tracking if the spot moves. No later workers have claimed to observe spontaneous eye movements. It was thought possible that the field fixation reflexes might operate when a rabbit moved about on an extensive slope and bring the plane of the visual streak projection into alignment with plane of the slope. In order to test this, the animal was placed inside a large drum, 1 m. /

1 m. in diameter, which could be rotated about its horizontal axis. Electronystagmography electrodes were placed so as to detect vertical movements of the eyes. The drum was arranged to be half black and half white thus presenting an artificial horizon to the animal. No eye movements were detected when the lights were put on after a period of darkness in which the drum had been rotated up to 30° from the horizontal. Eye movements of 5° induced via the labyrinthine reflexes could readily be detected with the apparatus. No head movements occurred. It was felt that the laboratory environment might be in some way inhibiting the animal from performing naturally so a rabbit was taken to Arthur's Seat in central Edinburgh where there are numerous extensive grassy slopes which stand well above the trees and vertical contours of the city buildings. Direct and ophthalmoscopic observation of the eye position showed that, even on steep slopes, the plane of the visual streak must be arranged perpendicular to the direction of action of the Earth's gravity.

In the apparent absence of any visual space reflex which adjusts eye position when the animal is on slopes, it appears that only one possible mechanism for directing the visual streak could remain but its operation would only be manifest after the animal's attention or interest had been aroused. de Kleijn pointed out that compensatory eye movements upon rotation of the head about its occipito-nasal axis were adequate to maintain eye position constant over a range of 20° in each direction. Outside this range an error appeared. It was concluded that the animal might obtain some deviation of the eye from its normal position by twisting the head to an angle beyond that at which complete compensation was obtained by eye movements in the opposite direction. The eyes would then begin to follow the rotation of the head.

A free standing rabbit was placed on top of a filing cabinet. Another rabbit was placed in an open basket some five feet away from the base of the filing cabinet. The animal sitting on the cabinet was then observed and photographed from the nasal end while it watched the activity of the rabbit in /

in the basket below. It was immediately clear that the observer rabbit rotated its head about the long axis when examining the animal in the basket. Head rotations of up to 40° were observed. These movements were not related to olfactory searching and the ears were not in such extreme positions that head movements would be required to bring them to bear on the rabbit in the basket.

With the head movements observed, however, the eye would have to rotate by at least as much as the head if the image of the other rabbit were to be brought on to the visual streak. As the first 20° of head rotation are not accompanied by eye movements then, in a 30° head rotation, we could expect, at most, a 10° eye rotation in the same direction. In fact the compensatory eye movements do not cease after 20° of head rotation so that the eye rotation actually achieved might be considerably less than 10° in 30° of head rotation. The mechanism suggested above might suffice for the voluntary attainment of small eye movements which may be required to transfer an image from the blind strip of the rabbit eye to a region bearing ganglion cells but does not appear adequate to supply extensive voluntary movements.

Upon careful examination of the photographs it was noticed that the eyes appeared to be rotating as much as the head. Further photographs were taken of the observer rabbit when his head was in a rotated position and were developed so that the plane of the iris was clearly visible. It was mentioned earlier that the plane of the iris tilts back somewhat more than that of the corneo-scleral junction (p. 2). Examination of figs. 104 A, B shows the position of the iris plane in the animal whose head is in the normal orientation. In fig. 104 C the head of the rabbit has been forcibly rotated through some 40° . The position of the corneo-scleral junction and partially visible iris shows that the eye is in its normal orientation. Apparently complete compensation for the head rotation has been achieved. In contrast, however, the photographs of a rabbit maintaining a voluntary rotation of the head show that the plane of the iris has rotated to the same extent as the head. This situation is shown in figs. 105 A, B, C. The eyes are clearly not stabilised /

stabilised under these conditions.

Such changes in eye position have not been observed in animals whose heads are held in the normal position. In view of the absence of spontaneous eye movements during other forms of testing it appears that voluntary head movements can offset the labyrinthine and neck reflexes so as to fix the eye in the head during rotation. The arrangement appears/complex means of achieving voluntary image tracking and clearly much more observation is required. The head rotating movements are difficult to stimulate and, so far, have been regularly obtained only when another rabbit to which the observer animal has previously been introduced is used as a stimulus. Some rabbits, perhaps through fear of their height, simply 'freeze' during the experiment and do not give head rotation. Curiously enough the animals situated on the floor have not been seen to look up at the observer rabbit.

Examination of the eye when the animal performs voluntary head rotation about a bitemporal axis suggests that the compensatory movements are effective. Only slight deviation of the long axis of the pupil was observed when the head pointed straight down.

Fig. 101 The visual field coordinates of the parallels whose projection is coincident with various ganglion cell isocount lines. ONH indicates the optic nerve head.

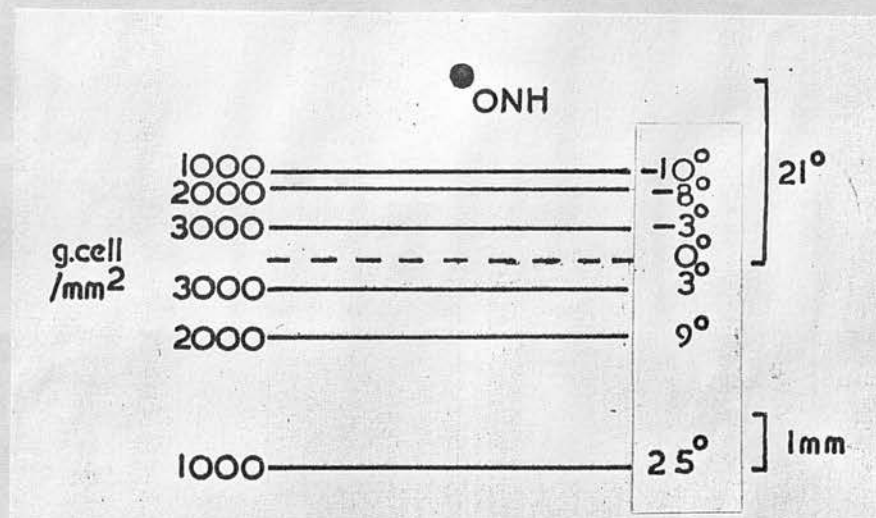


Fig. 102 Pictures after Magnus indicating the dependence of rabbit head position on vestibular rather than visual information (page 152). The inability of the sighted but bilaterally labyrinthectomised rabbit to right itself contrasts with the dog which is able to rectify its position by visual cues alone.

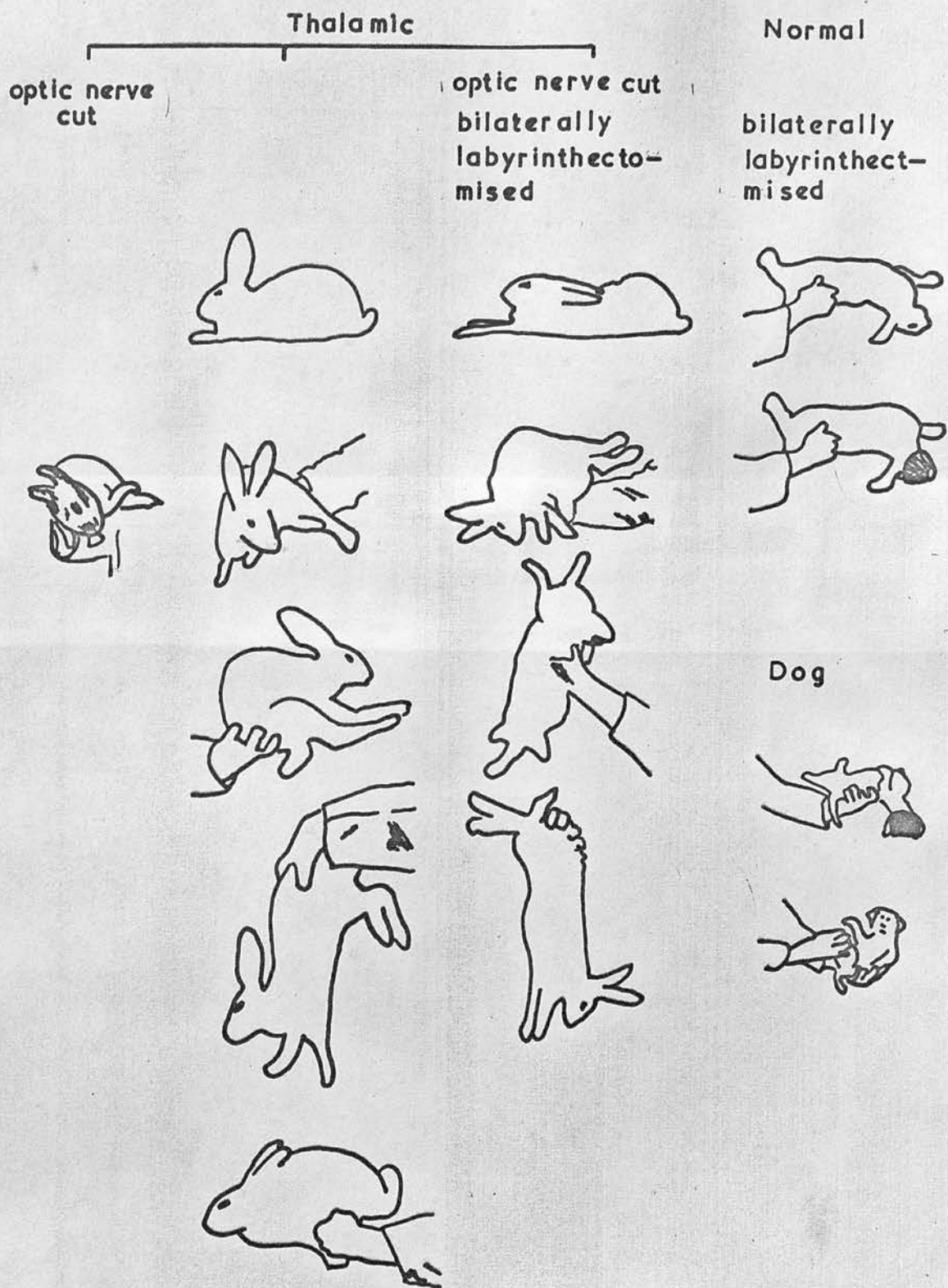


Fig. 103 The projection of the ganglion cell isocount lines along 10' radii in the case of a rabbit sitting with the anterior nodal point of its eye 6" above the ground. The hatched region indicates the projection of the myelinated band. The interrupted line indicates the medial boundary of the monocular field of that eye as determined ophthalmoscopically by light reflex (see page 153).

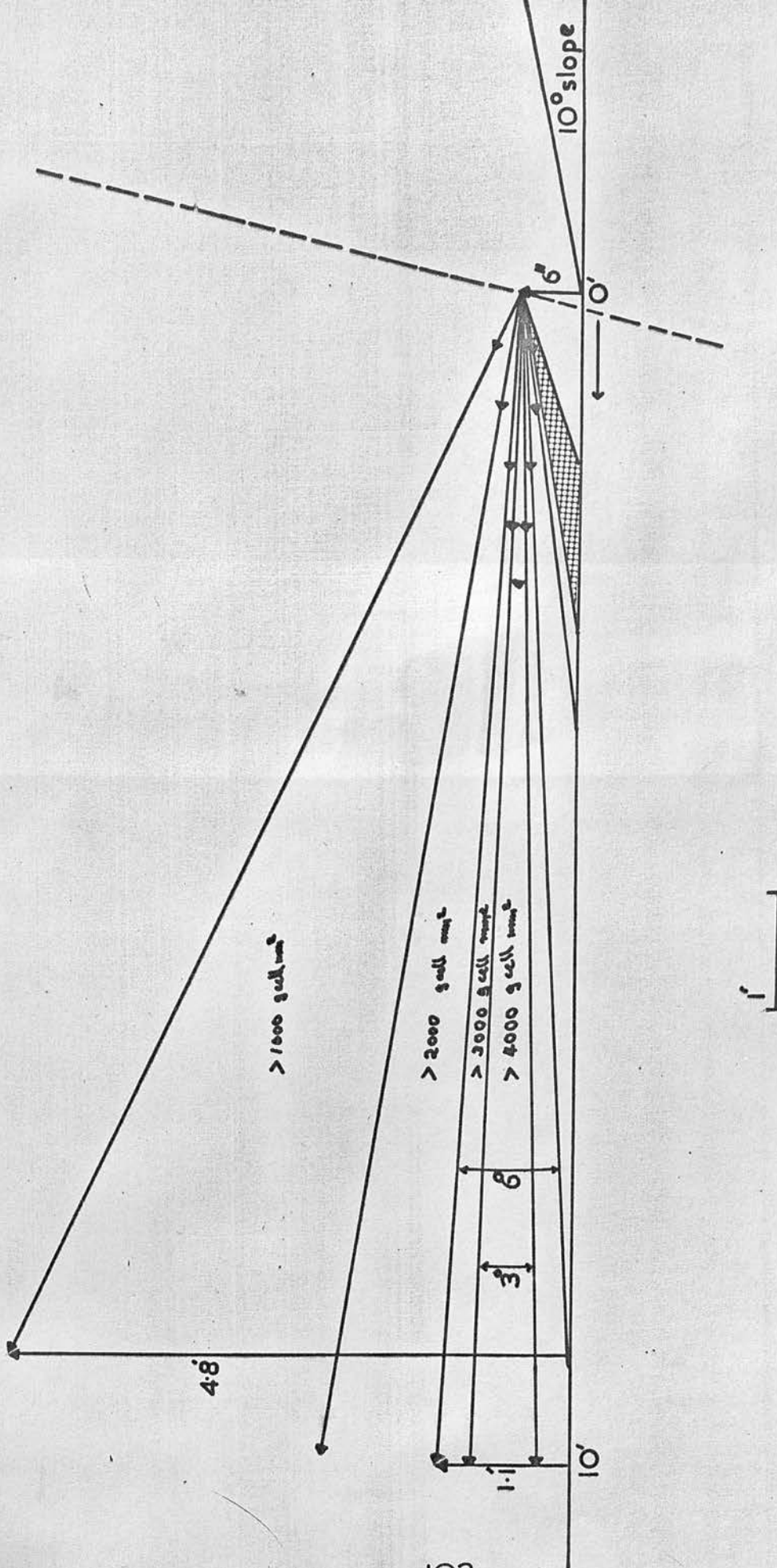


Fig. 104. A. and B. show, if carefully examined, the normal position of the iris of the rabbit eye when viewed from the front. The position is best seen in fig. 104B where the margin of the iris is more medially situated at the top of the eye than at the bottom.

C. and D. show the eye being maintained in its normal orientation, as indicated by the position of the upper and lower corneo-scleral boundaries, during forcible rotation of the head about its long axis. See page 155.



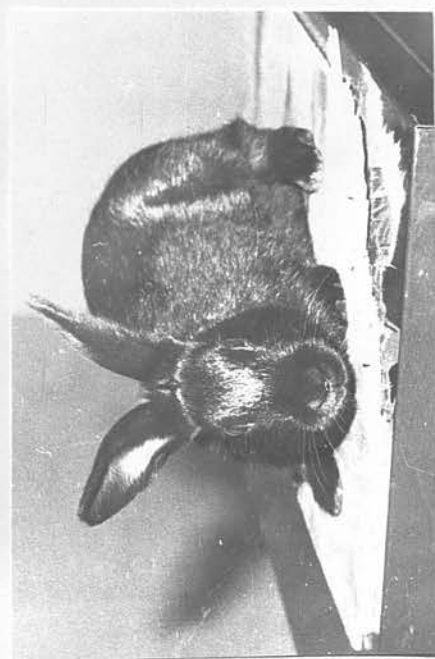
C



D



A



B

104

Fig. 105 A. The animal with marked head rotation viewing object below.

B. and C. A frontal view of the same animal under similar conditions to fig. 105A. The orientation of the iris in relation to the head in both photographs is similar to that in the animal with normal head posture shown in figs 104A and B. The eyes are thus 'locked' in their normal position within the head during voluntary fixation. See pages 155-156.



A



B



C



Edgar & Sons

PART II

Bond

TOP-SIZED-AIR DRIED

THE TOPOGRAPHY OF THE VISUAL FIELD PROJECTION
IN THE C.N.S.

MAGNIFICATION FACTORS

Under the conditions of the mapping experiments described in previous sections the optical system of the eye maps the three dimensional spherical coordinate system from the visual field on to the approximately spherical retinal surface. The distortion introduced by the optical processes is slight; it was noted in an earlier section that there might be some compression of the peripheral image (p.¹⁹) but this amounts to no more than 15%. The changes in photoreceptor density described on page 37 indicate that the maximum potential resolution at the peripheral retina is only $\frac{1}{3}$ of that in the area centralis. At the ganglion cell level the differential distribution of ganglion cells between area centralis and periphery is such as to make the maximum potential resolution at the periphery only $\frac{1}{50}$ of that in the area centralis. The columnar organisation of the retina ensures, however, that the map of the visual field projection that would be obtained from the ganglion cell layer is identical to that at the photoreceptor level. It would be expected, however, that if the regions of the C.N.S. which receive the retinal projections possess uniform cellular packing densities throughout their whole extent, then the projection of the visual field coordinates would undergo distortions determined by the retinal ganglion cell density for the region of visual field considered. The visual streak would thus be expected to receive a uniform and major representation while the extreme upper and lower field would occupy little area in the central representation. The representation would be expected to be nearly uniform along the streak but, as the ganglion cell count along the parallels decreases above and below the visual streak, it would be expected that the vertical meridia be widely separated on the projection of the visual streak itself but approach one another closely above and below the streak.

The concept of the topographic projection of the visual field coordinates on to the various stages of the central visual system existed on the basis of anatomical work for some time before Talbot and Marshall (1941) introduced /

introduced a quantitative means of indicating the relative extent of the representation of various portions of the visual field within a single projection. Subsequent to this, Daniel and Whitteridge (1961) initiated the use of the widely accepted magnification factor (M) as an index of cortical representation. This parameter is defined as the distance at some level in the visual pathway between the projection of two points subtending an angle of 1° at the eye. Variation in M indicates relative magnification throughout a specific projection or between projections at different levels of the C.N.S. A comparison of plots of magnification factor along various parallels and meridia in the representation of the visual field at some level in the C.N.S. with plots of the ganglion cell count along the equivalent parallels and meridia in the retinal projection of the visual field enables a test of the expectations outlined in the previous paragraph to be made. In many animals it has been found that the ganglion cell distribution appears to determine the value of M at various stages in the visual pathways. Absolute values of M in the maps at collicular, L.G.N. and cortical level have been presented earlier but for comparison purposes a set of M -factor distributions for these organs is included with the scales normalised to the scale of the ganglion cell distributions (figs. 106). For comparison with the results obtained from other animals the value of M has been measured in the horizontal (M_h) along the region bearing the projection of the peak ganglion cell count. In the vertical, M has been measured along the meridian which passes through the projection of the optic nerve head in the map considered (M_v). This arrangement corresponds to that in animals with a circular area centralis when the visual field coordinate system is centered on that area centralis.

The vertical ganglion cell counts are from three eyes and are taken along the meridian passing through the optic nerve head. The horizontal count has been taken along the peak count of the visual streak of one animal but other levels can equally well be chosen to show similar forms. The drop in count at the temporal end of the retina appears to correspond to the region /

region which deals with the binocular field and projects to the ipsilateral brain. This region occupies about 15-20° of monocular field and thus corresponds with about 2.5-3.3 mm. of the retina. The M factor measurements do not deal with binocular representation alone so that correlation of M and ganglion cell count for this region of the retina is not sought in those parts of the C.N.S. where binocular field is represented.

The plots of M_v and M_h for colliculus and cortex are directly derived from the map data. The distribution derived for the L.G.N. depends, however, upon the section considered. It was decided to average four M factor plots from different sections in order to arrive at one curve for comparison with other regions.

In the vertical plane the relationship between M_v and the ganglion cell count is striking at all levels of the rabbit visual pathways.

Along the horizontal, M_h and the ganglion cell distribution are obviously linked in the colliculus. In the L.G.N. there is a slight nasal increase in M_h while at the cortical level the increase in M_h in the nasal representation is accompanied by a marked decrease in M_h in the temporal region. Neither of these features is related to a change in ganglion cell density.

Other points indicate that the ganglion cell distribution is not the only factor determining the horizontal magnification factor. At all stations along the visual pathways M_h shows similar absolute magnitude along parallels above and below the projection of the visual streak and thus, instead of decreasing at the superior and inferior limits of the visual field, the meridional spacing remains constant. Again, in superior colliculus, L.G.N. and cortex it is found that the value of M_h and M_v at one region of the visual field projection differs considerably in spite of the fact that the region of retina receiving the corresponding retinal image may possess very similar ganglion cell densities in both directions.

The frog area centralis is a vaguely defined horizontal band (Chievitz, 1889), a little like that of the rabbit. Jacobson (1962) has shown that the tectal /

tectal M factor and the retinal ganglion cell count vary in the same way with retinal eccentricity along the vertical and horizontal. The arrangement is similar to that in the rabbit colliculus where M_h has a similar value along parallels which project on to regions of retina bearing different ganglion cell counts. In the pigeon tectum (Whitteridge, 1965) the area of surface allocated to the representation of the foveal region is proportional to the ganglion cell density. In the cat and baboon (Vejbaesya, 1967) the regions of expansion in the collicular representation follow the distribution of the areas of high ganglion cell density in the retina. The projection of the visual field meridia and parallels on to the rat superior colliculus reveals the presence of no marked expansions (Forrester & Lal, 1966; Kruger, 1966). The work of Lashley suggests the presence of a not very well developed area centralis (1932) which would thus not appear to be represented in the tectal projection. Some unpublished work by Forrester suggests that Lashley's findings are not correct and that the retinal ganglion cell distribution is uniform in the rat and this animal may thus not be an anomalous case amongst those studied.

Comparisons of M factor and ganglion cell densities for L.G.N. and visual cortex are not available in the published literature. Vejbaesya (1967) has, however, displayed Stone's retinal ganglion cell count (1965), Seneviratne's (1963) L.G.N. M_h determinations and his own M_h findings for the superior colliculus of the cat on one diagram with normalised scales. The correspondence between the curves is considerable. In another set of normalised curves he has compared M_h for baboon colliculus (Vejbaesya, 1967) and baboon visual cortex (Daniel & Whitteridge, 1961) with the centro-peripheral retinal ganglion cell density (Whitteridge, personal communication). In this case the relation between the factors is also clear.

In the observed cases other than rabbit, frog and possibly the pigeon anterior tectum it would appear that the proportionality coefficient between M and the ganglion cell density possesses a similar value along horizontal and vertical at a given point in the representation at all stations in the /

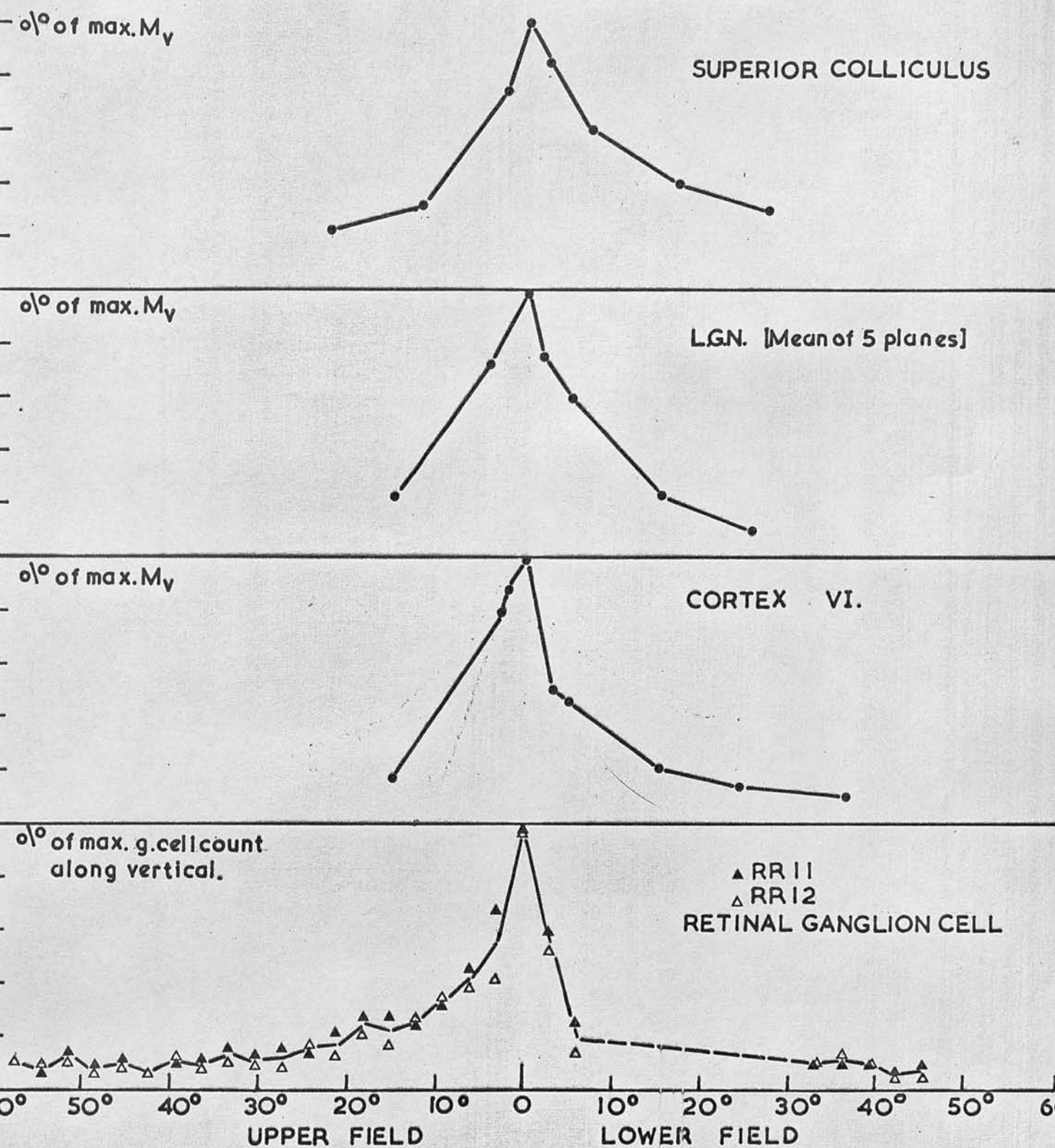
the visual pathway. In the rabbit and frog ~~some times~~ the value differs in the two cases. The generalisation that the area of a cortical sensory representation is determined by the appropriate peripheral receptor density, although apparently generally true, does not hold in the rabbit; at least along the parallels of the lateral geniculate and cortical representations.

The minimum absolute value for M to be found in the tectal maps of various animals is strikingly uniform. In rat M_h and M_v are about 0.02 and 0.04 mm/° respectively (Forrester & Lal, 1966). In cat, 60° out in the periphery, the value of M_h and M_v is similar at 0.02 mm/°. The same parameters in the baboon are 0.03 mm/°. The minimum value of M_v in rabbit is about 0.05 mm/° and M_h is constant at 0.04 mm/°. Even in the small tectum of the frog it is found that M_v and M_h have a minimum value of about 0.01 mm/°.

When averaged over the first 10° around the area centralis or foveal representation, it is found that the maximum absolute M is from 0.2 to 0.3 mm/° in baboon, cat and rabbit. The central regions of the area centralis representation may reach considerably higher magnifications in the order of 1.0 mm/° in cat and baboon.

No such similarity is to be found in comparison of the maximum M factors of the visual cortex maps in rabbit, cat and baboon. The peak value of M_v in rabbit is about 0.5 mm/°, in cat it is nearly 1.5 mm/° and in baboon the figure reaches some 7.0 mm/°. These figures may reflect the presence of a greater disparity of function between the visual areas of the above animals than is to be found between their superior colliculi.

Fig. 106 Normalised plots of the vertical magnification factor of maps from the superior colliculus, L.G.N. and cortical area VI. The plots are presented for comparison with the normalised plot of the ganglion cell density along the central vertical meridian.



VISUAL FIELD ELEMENTS AS PERCENTAGE OF TOTAL REPRESENTATION

Plots of the magnification factor along perpendicular axes suffice to show the extent of the influence of the ganglion cell density count on the representation of the visual field at various stations in the C.N.S. More extensive measurements are required for the determination of the overall distortion at each stage in animals, such as the rabbit, whose central visual field representations are far from uniform. In the case of the rabbit L.G.N. it is apparent that the M factor for any particular region of the field depends critically upon the plane of the section considered. It was decided that the overall form of the projection map would be more satisfactorily indicated by expressing the volume of tissue devoted to the representation of a given fraction of the visual field as a percentage of the volume containing the whole projection. In the superior colliculus and visual cortex the visual field is projected on to a sheet of cells whose uniform thickness and columnar organisation make it possible to use areas of surface to represent volumes. When expressed in percentage form as suggested above it is possible to compare the representation of the visual field on these organs with that in the non-uniform sheet of L.G.N. cells. This percentage measure has some physiological significance because, if we assume a roughly equal packing density of cells throughout the tissue receiving the visual projection at one stage, then the figure derived gives an approximate figure for the proportion of cells in the total representation dealing with the specific region of visual field considered. Such a figure cannot be derived from the presently available anatomical data.

For quantitative comparison of the maps it was decided to subdivide the visual field into 12 parts. The maps were divided into upper, lower and streak sections along the meridia. Along the horizontal the total map representation was divided into four parts of equal length, posterior temporal, anterior temporal, posterior nasal and anterior nasal field. The procedure is only made possible by the use of the standard eye positions but in spite of this some small discrepancies occur in the representation of the peripheral field at different stations which make the use of a more extensive subdivision rather unreliable.

TABLE IX Elements of visual field representations at various stations in the visual pathway as % of the total area or volume of tissue at that level.

T post	T ant	N post	N ant	
<u>Superior Colliculus</u>				
8	8	6	6	U 28%
9	9	11	16	S 45%
6	6	6	9	L 27%
23	23	23	31	
<u>L.G.N.</u>				
5.5	5	4.5	5	U 20%
11	13	14	23	S 61%
3	4	4	8	L 19%
19.5	22	22.5	36	
<u>Visual Cortex</u>				
2	4	4	8	U 18%
4.5	10	18	26	S 58.5%
2.5	3	5	13	L 23.5%
9	17	27	47	

Elements of visual streak as % of total streak volume.

19.5	19.5	24	37	S.C.
18	21	23	36	L.G.N.
8	17	30	45	V.C.

Visual Streak Representation. Figure 101 shows that the 2,000 g. cell.mm² isocount lines span the region of the visual streak in which the ganglion cell density is symmetrically distributed about the peak value in the vertical axis. These isocount lines coincide with the projection of the -8° and 9° parallels on to the retina. In the M factor plots along the vertical meridian it is clear that the expansion is also symmetrically distributed about the 10° and -10° parallels in the various projections of the visual field so, for convenience, these were arbitrarily chosen to represent the visual streak. At all levels the representation of this chosen part of the field receives the greatest magnification.

From the table III page 36 it may be calculated that 55% of the retinal ganglion cells lie within the 2,000 g.cell.mm² isocount lines (average of 3 retinal counts). It is of interest to note that the defined streak region of the L.G.N. and visual cortex maps, 10° to -10° parallels, receives the similar percentage of 61% and 59% respectively of the total representation. The superior colliculus map contains a more extensive representation of the visual field and the streak region occupies only 45% of the total. It is possible that this may indicate the projection to the superior colliculus of a different population of retinal ganglion cells to that sending axons to the L.G.N. Such an arrangement has been suggested in the case of the cat (Bishop & Close, 1955).

Upper and Lower Field Representation. Measurements, made on a three dimensional model of the rabbit retina which was constructed from a photograph of the squash mount RR7, indicated the following dimensions for the extent of the retina:

Optic nerve head to inferior ora serrata	18.5 mm.
Optic nerve head to superior ora serrata	8.3 mm.
Nasal to temporal ora serrata at level of visual streak	30.0 mm.

Assuming the general validity of the figure 0.167 mm/° throughout the retina then these figures suggest that the projection of the visual field at various /

various levels in the C.N.S. should extend in the vertical plane from the projection of the optic nerve head for 50° into the inferior field and 110° into the superior field. In coordinates centred at the visual streak peak count, these limits would be -70° and 90° respectively. The schematic eye indicates that the representation should extend from -75° to 105° in maps at central stations. Retinal measurement indicates that 180° (30 mm. on retina) project on to the retina which is a somewhat smaller figure than the 195° suggested by the schematic eye. The differences between the field extents indicated by retinal measurements and by the schematic eye are readily accounted for by the probable occurrence of some retinal shrinkage and the lowering of the value $0.167 \text{ mm}/^\circ$ near the periphery. It may thus readily be calculated that the region of the retinal image from 10° to -10° occupies 11% of the total retinal area. The upper field image is 55% and the lower field 36% of the total. The table clearly shows that percentage of the total visual representation devoted to the streak at central regions of the visual paths is considerably larger than that at the retina. The representation is increased by a factor of about 4.8 in the superior colliculus and by 6 in the L.G.N. and visual cortex. The upper and lower field representations at central stations obtain only half of their total retinal percentage while the upper field is more compressed than the lower in spite of the fact that the retinal ganglion cell density along the vertical falls off more slowly towards the lower retina (upper visual field) than the upper retina. This is one of the more puzzling findings in the work on both the geniculate-cortical and the collicular maps. In spite of the fact that 55% of the collicular map is devoted to regions off the visual streak compared with 40% in L.G.N. and cortex, the collicular representation compresses the upper more than the lower field in the same fashion as maps in L.G.N. and cortex. In the L.G.N. the upper field representation is confined to a limited volume of tissue at the anterior end where it has been observed to extend as far as the 80° parallel. In the visual cortex the representation above the 20° parallel has not been seen but may lie over the posterior pole as is suggested by the cytoarchitectonic /

cytoarchitectonic evidence (Rose, 1931; Brodmann, 1909). It is unlikely, however, that the representation will be extensive since the L.G.N. volume dealing with that region of the visual field is very small. The extensive monocular upper field determined ophthalmoscopically by the retinal light reflex must have a very limited central representation, which, of course, may be all that is required for the generation of a 'freeze' response to objects in the sky. The situation in the rabbit is very similar to that in the cat where the upper field representation occupies only 40% of the total superior colliculus area (Vejbaesya, 1967), 33% of L.G.N. (Seneviratne & Whitteridge, 1962) and 37% of the visual cortex (Bilge et al., 1967), in spite of a similar ganglion cell distribution in upper and lower retina.

The mapping data makes it clear that the superior colliculus has a representation of a larger part of the visual field on a more uniform scale than the geniculo-cortical pathway. This arrangement lends weight to the suggestion, which is developed later, that the superior colliculus acts as an 'observer' or 'early warning station' for events in the visual field of the animal.

Expansion of the Nasal Field Representation. In the superior colliculus and L.G.N., each of the three more temporal quarters of the visual field ^{as divided on page 162,} show a similar representation which is in the order of 22% of the total map. The nasal anterior quarter of the field is, however, larger and occupies 31% of the total field in the superior colliculus and 36% in the L.G.N. The corresponding region of retina shows little evidence of an increased ganglion cell density other than a widening of the 1,000 g.cell/mm² isocount band.

The nasal quarter of the L.G.N. differs from the other parts of the visual field representation in that it receives the projection of the ipsilateral fibres from the most temporal 15° of retina which deal with the binocular field. This region of the L.G.N. must therefore accept the projections of ganglion cells in 60° instead of 45° of retina. If we assume that the organisation of region of retina with uncrossed projections is similar /

similar to the remainder of the organ then it becomes possible to predict that each of the three more temporal quarters of the visual field should receive 23% of the central representation, instead of 25% and the nasal quarter of field should receive 31%. This is near to the 36% observed.

The presence of an expanded representation of the nasal field in the collicular map when there is an apparent absence of an electrophysiologically determinable ipsilateral projection argues against the above theory. In 1911, however, Loepp demonstrated the presence of ipsilateral fibres in the stratum opticum of the rabbit superior colliculus so that such fibres may be present although not at present electrophysiologically demonstrated. The above explanation is thus not entirely eliminated. The increase in the representation of the nasal field in the superior colliculus appears, however, to come about as a result of an increase in the vertical magnification factor. In the L.G.N. it results from an increase in the horizontal magnification factor. It may thus be that the explanation is valid in L.G.N., because the expansion would be expected to arise from change in M_h , but some other basis exists for the collicular expansion.

In the visual cortex the nasal quarter of the visual field receives 47% of the total representation which is at least 10% more than achieved at the lower levels in the system. The increase may result from the presence of the transcallosal projections bearing the extreme nasal field representation. The presence, however, of a marked compression of the temporal field representation (the temporal posterior quarter receives only 9% of the total VI area) makes it clear that other factors intervene in determining the extent of the representations. It is very likely that there are, for instance, considerable variations in the degree of convergence of L.G.N. fibres in different regions of the visual cortex.

Single units of the expanded cortical representation of the nasal field might be expected to be more sophisticated than those of other regions of the cortical representation or, at least, to form a population of different composition, because this part of the visual field is of considerable importance to the moving animal. Specialisation of single units in the /

the nasal region of the cortical map has not yet been observed except in that cells responding to binocular input are confined to this region.

Behavioural evidence suggests, however, that rabbits do not use the nasal field for the detailed examination of objects. Washburn and Abbott (1913) point out that rabbits undergoing visual testing survey the problem monocularly with alternate eyes. They concluded that when a rabbit turned its face to one of the test stimuli it was, in fact, looking monocularly at the other. Out of 50 trials lettuce was taken on only two occasions from a region in front of the nose when pieces were held simultaneously in the nasal and lateral fields. On the other 48 occasions the animal turned to eat the food held at its side.

These findings are apparently confirmed by stories of rabbits colliding with people who stand in their runs (Thompson, 1933) or of rabbits, undergoing jumping tests, which collide with the hurdle if it is set to a new height (Breland & Breland, 1966). Such examples suggest a peculiar neglect of events in the binocular field although it would be quite wrong to suggest, as do Breland and Breland that

"Apparently rabbits rely very little on visual cues in finding their way around",

for under these conditions, in the run or the experimental laboratory, the animal may regard the situation as familiar so that path habits come to the fore in regulating its locomotor activity. The path habits of the rabbit appear to be like those of the water shrew as described by Lorentz (1952). When running a familiar path, the shrew will jump over a space previously occupied by a stone which has been removed. Lorentz points out that rats are more flexible in their behaviour and would not carry out such an action. Dependence upon path habits during flight does not, however, indicate failure to use vision under normal or novel circumstances and we cannot conclude that the nasal field plays no role in rabbit detail vision although the predominance of monocular observation suggests that its contribution is minor and that the nasal expansion exists to facilitate some other function.

The /

The obvious suggestion, which follows from the previous description of the projections to the region, is that the nasal visual field and associated visual cortex are used as a range finder which is brought to bear on important stimuli by means of the appropriate head movements. The confinement of the expansion within the nasal region to an increase in horizontal magnification factor is thus to be regarded as a result of the extra binocular and callosal projections rather than as a means of equalising the horizontal and vertical magnification factors in a region specialised for pattern vision. The mechanism of disparity facilitation, at fixed convergence, of binocular receptive units which has been suggested by Barlow, Blakemore and Pettigrew (1967) as the basis of depth discrimination in the cat would equally well suit the rabbit in which convergence movements have not been described. Hubel and Weisel (1968) are unable to confirm the results of Barlow et al. in the cat but no examination of binocular cortical units has been made in the rabbit.

The callosal fibres of the nasal field representation in the visual cortex are envisaged as carrying out the other role peculiar to this region which is that of linking the two halves of the visual field. This role for the fibres has been suggested by Whitteridge for some time (1965) and was recently confirmed by Hubel and Weisel (1968) who mapped the receptive fields of single callosal fibres in the cat. They found all the callosal units to have receptive fields passing across the vertical meridian which represents the decussation line in that animal.

The central region of the VI representation, which deals with the lateral visual field receives a lesser, but in absolute terms quite extensive area than the cortical region dealing the nasal field. The area devoted to this region of the field is great enough to support the view that it is concerned in the analysis of pattern and shape recognition. At one time the author had some suspicion of the presence of a specialised region of the area centralis which dealt with the lateral area but this appears to have been ill founded.

At /

At retinal level, within the visual streak, there is no evidence from ganglion cell counts which would support the differentiation of function suggested between the central and nasal field representation on the visual cortex. As has been shown the evidence for this is anatomical and behavioural. It may be, however, that the cortical apparatus for pattern vision in these two regions is equipotential because the extra duties imposed on the nasal field representation do appear to be accommodated by some increase in available cortex. Such problems can only be answered by behavioural work and studies of differential unit distribution in retina and cortex. It is not envisaged that nasal region of the visual streak representation in the superior colliculus differs much in potentiality from other regions of the centralis projection.

The more compressed temporal region of the cortical streak representation enables exploitation of the animal's potentiality for panoramic vision at the cortical level. It is suggested that the extent of this area is just adequate for the analysis of a stimulus in the posterior field in sufficient detail for an estimate to be arrived at, when the rabbit is in the "freeze" condition, as to the safety of turning the head so as to bring the lateral field to bear upon the stimulus.

CENTRAL REPRESENTATION OF THE AREA CENTRALIS IN RABBIT AND CAT.

It is of interest to compare the representation of the area centralis in the rabbit and cat. The definition of the visual streak of the rabbit as the region of retina between the projections of the 10° and -10° parallels has been shown to correspond approximately to the equation of the streak with the retina bearing a ganglion cell count greater than $2,000 \text{ per mm}^2$. The definition of an area centralis in the cat which may be compared with the streak of the rabbit is not straightforward if it is hoped to obtain figures of functional significance. In view of the fact that the extent of central representation usually appears to be predominantly determined by the retinal ganglion cell concentration, it is import, for simplicity, that regions of retina /

retina bearing a similar range of ganglion cell densities should be chosen for comparison. The elongated form of the rabbit area centralis involves so many cells that the alternative of selecting a limited strip containing a similar percentage of the total ganglion cell count of the retina to that found in the cat area centralis would mean ignoring the representation of the greater part of the streak whose functional importance is undoubted. An examination of the distribution of ganglion cells along the vertical in rabbit and cat retina reveals that the choice of the 2,000 ganglion cell/mm² isocount to define the area centralis of the cat marks off a region of retina which has an anatomical reality equivalent to that in the rabbit (see fig. 37 and fig. 3 of Stone, 1964). The results presented below, which are obtained upon the basis of the above definitions are of a form which clearly indicates that they do not result from the arbitrary nature of the area centralis boundaries but reflect a real difference in the organisation of visual information processing in the cat and rabbit. It should be noted, however, that Stone has chosen to define the cat area centralis as the region of retina with a count over 3,000 g.cell/mm².

Areas in the table below have been obtained from my own data for the rabbit or by measurement of diagrams given by Stone (1964), Bilge et al. (1967) and Vejbaesya (1967) for the cat.

Area Centralis as a % of the Total Representation
at Various Levels of the Visual Pathways

	<u>Rabbit</u>	<u>Cat</u>
Retina	14.0	0.35
Superior colliculus	45.0	10.0
Cortex (VI)	60.0	28.0

The percentage of the total retinal projection occupied by the rabbit area centralis is thus three times greater in the superior colliculus than in the retina and four times greater than in the retina at cortical level. In the cat, however, the corresponding figures are 26 and 80 times. The ratios are, of course, averages for the whole area centralis and in the rabbit cortex /

cortex, for example, regions could be found within the centralis representation which differ by a factor of 5 in their magnification.

Consideration of the actual areas involved emphasises the difference between the rabbit and cat.

Area of the Centralis Representation at various
levels of the Visual Pathway (mm²)

	<u>Rabbit</u>	<u>Cat</u>
Retina	82	2.5
Superior colliculus	16	3.4
Cortex (VI)	28	42.0

Thus, the area of the collicular representation in the rabbit is about $1/5$ and the cortical $1/3$ of the retinal streak area. The area of the collicular representation in the cat is, by contrast, 1.3 times that in the retina and in the cortex is 17 times greater. In spite of an increase in the percentage of the total representation devoted to the area centralis at all stages in the visual paths of rabbit and cat, there is an absolute increase in the area of the representation only in the case of the cat. The effect of this difference between the cat and the rabbit is best revealed in functional terms by the following calculation.

In the rabbit, 1 mm^2 of area centralis projects to 0.34 mm^2 of visual cortex (average for whole streak projection) while a similar element of the cat retina projects to 17 mm^2 of cortex. The visual cortices of the two animals are similar in thickness (O'Leary & Bishop, 1938; O'Leary, 1960) while their cell densities are in the same order of magnitude (Cragg, 1967) so that 1 mm^2 of retina projects to an area of cortex 50 times larger in cat as in rabbit and containing 50 times as many cells for the analysis of the retinal output.

Because of the difference between the FND of the rabbit and cat eye, points 1° apart in the visual field are separated by a distance of 0.25 mm in the cat and 0.167 mm in the rabbit retinal images. The area of a 1° square in the retinal image is consequently 2.25 times greater in the cat as in the rabbit /

rabbit eye. The cortical representation of a 1° square of visual field on the cat visual cortex is thus 50×2.25 or 112 times larger in area than on the rabbit cortex (0.01 mm^2 per square degree in rabbit; 1.1 mm^2 per square degree in the cat). It is to be emphasised that cell density at the cortical and retinal ganglion cell level is similar, for the regions considered, in both animals. The variations in cortical magnification along the representation at the rabbit visual streak means that a 1° element in the expanded representation of the nasal field may have an area which is as much as $1/45$ of that in the cat!

A similar calculation reveals that a one degree square of visual field which projects on to the area centralis is represented in the superior colliculus of the rabbit by $1/15$ of the volume of tissue to be found in the cat.

The total surface area of the superior colliculus is very similar in cat and rabbit (about 35 mm^2) but because of the difference in the area of visual cortex in the two animals, the superior colliculus of the rabbit is nearly 60% of the area of the visual cortex while in the cat it is no more than 5-6% of the visual cortex area. We might thus expect the superior colliculus to make a greater contribution to the overall visual behaviour of the rabbit than is the case in the cat.

The fact that the cortical representation of the rabbit area centralis possesses fewer cells than that of the cat to deal with each 1° square of visual field does not necessarily indicate that its cortical units will require less sophisticated adequate stimuli than those of the cat. The rabbit might, for instance, carry on a cortical analysis similar to that of the cat but at lower resolution. In earlier sections, however, it has been shown that the single units of the rabbit visual cortex are of simpler organisation than those of the cat cortex. The differences between rabbit and cat visual cortex units requires more detailed examination and will be taken up again.

Any attempt at relating the behavioural differences between rabbit and cat /

cat to the form of their central visual projection must take into account the differences in magnification factor along various axes of the visual field projection. The most noticeable feature at all levels of the rabbit visual system is the differential magnification along the vertical and horizontal of the visual field projection. From another part of the discussion we find that the ratio of M_v/M_h for a region at the centre of the visual streak projection is about 7 in the superior colliculus, 9.3 in the LGN and 10 in the visual cortex. In the cat the ratio is very close to 1.0 at all levels. It is clear that the difference between the two animals in regard to the area of the centralis representation does not arise from symmetrical differences in magnification. Along the vertical the averaged cortical M_v factor for the streak, 0.3 mm/° , is not much less than that for the cat area centralis representation, 1.0 mm/° . The value of M_h at the streak centre, 0.03 mm/° is considerably less than the 1.2 mm/° value of the cat. The difference in the area of representation of a 1° square on the visual cortex of cat and rabbit thus arises predominantly from the small scale of the representation along the horizontal on the rabbit cortex. The number of cells available for the cortical analysis of the vertical component of a retinal image would thus be similar in the two animals but very different in respect to the horizontal component.

The visual resolution of the rabbit has been determined by Von Hof (1957) to be about $15'$. Examination of the protocol shows, however, that the experiment may have revealed vertical or horizontal acuity depending upon the animal's interpretation of the experimental requirements. It is thus not known whether the differences between M_v and M_h in rabbit cortex and colliculus are reflected in differing horizontal and vertical resolution. Von Hof has not carried out controlled experiments to determine whether a difference exists (personal communication). An investigation into the matter in cooperation with Von Hof is envisaged. For the present we can only note that the movements of vertical OKN are smaller than those of horizontal OKN (Brecher, 1964). This finding obviously supports the suggestion /

suggestion of differential treatment of vertical and horizontal components of the visual stimuli. It is, however, like the observation that the eye muscles for vertical movement are much larger than those for horizontal in that little further significance may at present be attributed to the information.

SERIES AND PARALLEL DATA PROCESSING

The cat carries out a detailed analysis of its visual environment by bringing small portions of the visual field by means of eye and head movements to bear successively on the restricted area centralis. Such sequential analysis would be referred to in computing terminology as 'serial data processing'. Serial analysis is economical of components and inter-connecting pathways but entails sequential input and data transfer so that it contrasts with a 'parallel' processing system in that considerably more time is required for the input of a given amount of information. In the case of the cat visual system, a further problem arises in that the scanning movements of the eyes and head result in the projection of the visual field coordinates shifting about on the visual cortex. The need, under these circumstances, for a transformation of the retinocentric to a spaciocentric image and for a means of integrating successive detailed glimpses of the environment into a single picture has already been mentioned. It is clear that these necessary extra steps in serial processing must involve the passage of more time before they are concluded.

It has been shown that, contrary to previous belief, the rabbit can indirectly obtain voluntary eye movements in both horizontal and vertical plane and may in this respect be regarded as similar to the cat. This behaviour is, however, apparently unusual and it is noteworthy that the rabbit, whose survival depends upon obtaining early warning of danger and subsequently upon deciding at each instant between the survival value of immobility or flight possesses a visual streak which, without the giveaway eye or head movements of the serial system, enables the animal to carry on a real-time /

real-time, simultaneous analysis of 360° of visual field at and near to ground level. The rabbit visual system is predominantly equipped to act as a parallel data processor which possesses the important feature of speedy collection and transfer of information.

The advantages of parallel processing are clear. The disadvantages are more difficult to deal with but stem from the usual drawback of the parallel computing system - the need for large numbers of peripheral and central components.

If we accept Stone's (1964) figure of 90,000 ganglion cells in the whole cat retina and my own optic nerve count as indicating the presence of 270,000 ganglion cells in the rabbit retina, then table II of page 36 enables us to calculate that the region of retina outside the area centralis (2,000 g.cell/mm² isocount line) contains 80,000 ganglion cells in the cat and 115,000 ganglion cells in the rabbit. Of the 180,000 ganglion cells possessed by the rabbit retina in excess of the cat, some 160,000 are thus located within the parallel processing area centralis. The serial processing cat area centralis contains only 10,000 ganglion cells.

It is, of course, true that all retinæ may be regarded as parallel data processors one sense because the peripheral retina is simultaneously acquiring information from a large portion of the animal's visual field. It is of interest to note that the evidence suggests that, unlike the area centralis, the peripheral retina is organised in similar fashion in rabbit and cat. The total number of peripheral ganglion cells is similar in the two species and, averaged overall, the peripheral retina may be calculated to contain the same density of six ganglion cells per square degree of visual field projection in cat and rabbit. The demands for central representation of this parallel processing system are limited by the low ganglion cell densities which exist in the relevant portions of the retina. The very nature of the rabbit visual streak, which intrinsically involves high ganglion cell densities, obviates this means of limiting the demand for visual cortex.

A possible reason for the compression of the visual field projection along /

along the horizontal in the various central representations must now be clear. The elongated rabbit area centralis, wide visual field, acute hearing and flight pattern have proved to be a successful adaptation. An equilibrium will have been reached in which we may assume that M_v and M_h for the various regions and the magnitude of the area of cortex allotted to visual function are balanced against one another. If the horizontal representation of the visual streak were to be at the same scale as the vertical, and proportional to the ganglion cell count, as it is in the cat, then it would occupy a region of visual cortex some 50 mm long by 6 mm wide. In the rabbit ecological niche there is presumably little premium for the sophisticated analysis of the horizontal component of the retinal image so that the advantage of all round vision has been retained, without the need for a huge visual cortex, at the expense of horizontal resolution. The usual near equality in vertical and horizontal of the proportionality coefficient between ganglion cell density and magnification factor has been abandoned in the rabbit with the central horizontal compression of the representation to fit the available cortex. A similar argument applies to the superior colliculus.

We thus arrive at a somewhat paradoxical arrangement in which a compression of the cortical and collicular visual field representation along the horizontal results from a lateral extension of the area centralis. Why should the potentiality for high resolution along the horizontal be provided in the retina if advantage of it is not taken in more central regions? An extensive visual field representation can be obtained, after all, without the need of an extended area centralis. It is possible that the convergence of inputs in LGN, cortex and superior colliculus increases sensitivity in some fashion or perhaps the high ganglion cell density of the visual streak is there to serve the needs of vertical rather than of horizontal analysis. An examination of the properties of the rabbit retinal single units suggests an alternative explanation which is developed in the subsequent section.

SPECIES DIFFERENCES IN RETINAL
GANGLION CELL RECEPTIVE FIELDS

Recordings of single fibre activity in frog retina were first obtained by Hartline (1938; 1940). The responses to the flashing of a light spot shining on a limited region of retina fell into three classes; a discharge might be elicited when the light was turned

1. on
2. off
3. on and off.

The description was extended by Barlow (1953) who found that the illumination of a region surrounding the excitable field of on-off units, but not pure off or on units, could inhibit the response to light on or off stimuli applied to the field centre. Contrary to the statement by Barlow (1953, discussion) this lateral inhibition had been observed and measured by Hartline (1940, fig. 3b, p. 704), which does not appear to be generally recognised, but its spatial organisation was not appreciated. Similar types of unit were recorded from the optic nerve of the rabbit by Thompson (1953).

The discharge pattern of the large ganglion cells of the cat in response to punctuate light stimuli applied to the retina fell into three categories similar to those found in the frog (Kuffler, 1953). The spatial organisation of the excitatory regions of the single unit fields revealed, however, that the three forms of response arose from two types of receptive field. Kuffler showed that a light spot shone in the centre of the receptive field would, if small compared to the field size, elicit a response when turned

1. on
- or 2. off

but not on both occasions. These circular areas were surrounded by an annular region from which a response could be obtained during the opposite phase of illumination to that exciting the central region. The centre and surround would, if simultaneously stimulated, inhibit one another. On-off response to diffuse illumination arise through stimulation of centre and surround together. This form of receptive field is described as concentric.

The /

The early work of Hartline and Kuffler tended to emphasise the on-off response properties of the retinal units. The output of the ganglion cell matrix came to be regarded as a rather coarse representation of the light and dark areas of the original retinal image coded in the form of a mosaic of impulses in the optic nerve. The interpretation of the optic fibre message was conceived in terms of a central analysis of the on-off activity in the incoming fibres (Granit, 1956).

The naturalistic approach to the interpretation of retinal function originated in Barlow's 1953 paper rather than in, as is usually claimed, the more spectacular contribution of Lettvin, Maturana, McCulloch and Pitts (1959) who extended and formalised the method.

Barlow (1953) and Lettvin et al. (1959) comment on the apparently paradoxical combination of an efficient optical system and fine receptor mosaic with three different retinal projections of equally poor resolution of which two are apparently complementary. The similarity of this problem to that of the limited central representation of the elongated rabbit area centralis will be apparent. The thesis to be developed is that, in principle, the solution to both problems is the same.

Consideration of the results of his analysis, carried out with light spot stimuli, of frog retinal unit properties led Barlow (1953) to the conclusion that the on-off units were especially sensitive to the movement of small objects within their receptive field. He went so far as to call them fly-detectors. The sharp optical image - and fine receptor mosaic - may help in the detection of movement and thus, since the units are not regarded as transmitting information about light intensity at some region, the apparent contrast in resolution between receptor and ganglion cell no longer appears perverse. Less convincing explanations of on and off unit activity were also given. Lettvin et al. took up this approach but in abandoning the concept of the retina as a simple sensor of light they also gave up the use of small light spot stimuli on the assumption that they may give accurate information about unit behaviour but at the same time be misleading as to the natural function of the units. The single units were regarded /

regarded as each being organised to respond to some specific, important feature of the frog's natural visual environment. The experimenter's role was understood to involve the selection, from the infinity of possible visual stimuli, of that which is the adequate form for a given unit under natural conditions - such a stimulus would be required to give rise to a response which is invariant under a variety of background conditions.

As originally described (Lettvin et al., 1959), the frog retinal units were analysed by naturalistic stimuli to give five classes:

1. Sustained edge detector (on)
2. Convex edge detector
3. Moving edge detector (on-off)
4. Dimming detector (off)
5. Dark detector.

In due course Maturana (1962) and Maturana and Frenk (1963) investigated the units of the pigeon optic nerve by similar methods to those used by Lettvin et al. (1959). Responses were found to be difficult to elicit with a light spot but more complex stimuli revealed a variety of unit types:

1. Verticality detector
2. Horizontality detector
3. General edge detector
4. Directional moving edge detector
5. Convex moving edge detector
6. Luminosity detector.

The analysis of Jacobson and Gaze (1964) suggests that the goldfish may possess a similar variety of retinal single units to the frog and pigeon.

Analyses of single units in the cat retina (Wiesel, 1958) and optic nerve or tract (Hubel, 1960a, b) failed to reveal the presence of any class of units other than the concentric form described by Kuffler (1953). Records made in the LGN of the cat (Hubel & Wiesel, 1961) also failed to reveal units with complex functions which tended to confirm the findings from the retina. Single units recorded from the cat visual cortex were found to require much more complex stimuli than those in the LGN or retina before a response could be obtained (Hubel & Wiesel, 1962; 1965). The spider monkey appeared to be similar /

similar to the cat in that it possessed concentric units alone although these showed special properties in relation to coloured stimuli (Hubel & Wiesel, 1960)

The difference between the retinal units of the frog, pigeon and goldfish and those of cat and monkey led Maturana (1964) to suggest the existence of two types of visual systems amongst the vertebrates, related to the presence or absence of neocortex;

"1. A deterministic system present in the amphibians reptiles and birds, in which the function of the ganglion cells is highly specialised and unambiguous. The fundamental elements of form, edges, corners, points, colour, movement, etc., are discerned at the level of the retina and are as such projected to the tectum.

2. An indeterministic system, found in mammals, where the output of each ganglion cell is unspecific, and ambiguous, the fundamental elements of form and colour being transferred to the geniculate and cortex as the combination of the output of a whole neighbourhood of ganglion cells.

The deterministic system is more economic, it requires less cells, but it is more rigid and can transmit a more restricted amount of information to the brain. The indeterministic system requires more cells in the brain but can do more complex operations on the fundamental visual information and is essentially more plastic and has greater possibilities."

The discovery that the rabbit retina, especially in the visual streak, possesses a greater variety of single unit classes (Barlow & Hill, 1963; Barlow, Hill & Levick, 1964; Levick, 1967) than that of the frog eliminated the distinction between the submammalian vertebrates and the mammals which had been drawn by Maturana. The rabbit retinal units formed at least nine classes:

1. On centre
2. Off centre
3. /

3. Directional on-off
4. Directional on
5. Large field off (shadow)
6. Horizontal edge detector
7. Vertical edge detector
8. Local edge detector
9. Uniformity detector.

It is perhaps of significance to note that nearly 25 classes of visual single units have been recorded from the optic lobe of the locust (Horridge, Scholes, Shaw & Tunstall, 1965). Thus in a form possessing relatively far less central tissue than is the case in the rabbit, frog or pigeon we find a greater variety of unit types than in the vertebrate group.

SOME SURPRISING RESULTS FROM THE CAT.

Hubel and Wiesel (1962) considered the possibility that the cat retina might contain single unit types, like those of the frog retina, which could have been overlooked because of the small size of their ganglion cell or axons. They summarised the generally accepted view at that time:

"If their fields are different from the well known concentric type, they must have little part to play in the geniculo-cortical pathway, since geniculate cells all appear to have concentric-type fields (Hubel & Wiesel, 1961). The principal cells of the lateral geniculate body (those that send their axons to the striate cortex) are of fairly uniform size, and it seems unlikely that a large group would have gone undetected. The smallest fibres in the cat's optic nerve probably project to the tectum or pretectal region; in view of the work in the frog, it will be interesting to examine their receptive fields."

The assumption that the smallest fibres in the cat optic nerve go to the superior colliculus alone is almost certainly incorrect. The area centralis of the cat has an extensive representation on the visual cortex and yet its ganglion cell population has the highest concentration of small cells in the retina and probably contributes a large proportion of the smallest axons /

axons to the optic nerve. The fact that the fibres reaching the superior colliculus are mainly those of small diameter is not a contradictory finding because these may be collaterals of those projecting to the LGN or the tapered extensions of larger diameter optic nerve fibres.

The first indication that complex receptive fields might have been overlooked in the cat retina was the discovery by Kozak, Rodieck and Bishop (1964) that 4% of the units recorded from the LGN possessed directional selectivity in their response to moving stimuli. An attempt to record such units from the retina (Rodieck & Stone, 1965a) failed. A companion paper, however, included a note describing the properties of a retinal unit which was inhibited from maintained activity upon the entry of black or white stimuli into its receptive field (1965b). Such units have come to be called uniformity detectors. In 1966 the presence of this type of unit was confirmed by Stone and Fabian who concentrated upon attempting to record from the ganglion cells of the area centralis.

Out of 50 units analysed in detail 16 were not of the concentric type. Ten were centre only, C, units which possess an inhibitory surround that does not respond to the flashing of a light spot. Two units possessed a small centre but large 15° surround. Three were on-off types while one directional on-off unit was discovered.

In view of these earlier findings it is odd that Barlow, Levick and Westheimer (1966) were so violent in their response to Spinelli's claim of discovering edge and bar detectors in the cat retina (1966). It is true that the claim to have found edge receptors extending more than 25° across the retina is one to induce scepticism but private enquiry on the part of Barlow et al. rather than public suggestions of hoaxing would have been more profitable. Spinelli (1966) replied to Barlow and in another paper described directional units and units responsive to luminous flux as present in the cat retina (Spinelli & Weingarten, 1966) but unfortunately the proportion of the total sample of 300 units which these formed is not given. More recently Spinelli (1967) has published a detailed paper on the cat retina./

retina. In this he concentrates on the more localised types of receptive field. Bar detectors, edge detectors and following units are reported along with a variety of complex fields which appear at high light intensities. 145 units were examined. 24% were not concentric types, i.e. 5.5% possessed no surround; 4.5% were bar or edge detectors and 14% were left unclassified.

RABBIT RETINAL UNIT POPULATION

At the present time (1968) single units with other than concentric organisation have been recorded from the retina of goldfish, frog, pigeon, rabbit, ground squirrel and cat. Concentric units alone have been reported in rat (Brown & Rojas, 1965) and monkey (Hubel & Wiesel, 1960) retina but neither report has been confirmed. It must also be borne in mind that the techniques used by Hubel and Wiesel were not adequate for the detection of the more complex types of unit in the cat retina. Thus, even if the attempt is premature, we are obliged to reconsider the distinction which has been made, and generally accepted, between the organisation of the rabbit visual system on the one hand and that of the cat and monkey on the other.

The table below contains a quantitative comparison of the proportion of concentric and non-concentric units obtained within the area centralis of the cat (Stone & Fabian, 1966), within 12° radius of the area centralis (Spinelli, 1967) and within the central region of the rabbit area centralis (Levick, 1967).

	<u>Cat</u>		<u>Rabbit</u>
	Stone	Spinelli	Levick
Concentric	68%	76%	42%
Not concentric	32%	10%	55%
Unclassified	-	14%	3%

The periphery of the cat retina has not been reported to contain any units other than the concentric type but in the rabbit only 48% of the units outside the area centralis are concentrically arranged.

Thus, in area centralis and periphery, the rabbit retina possesses a very /

very significantly smaller proportion of concentric units than does that of the cat. The information and statistics relating to rabbit and especially to cat must not be regarded as final. The population of rabbit area centralis units comes from the central region of the streak and may differ from that at each end. The results for the cat are only in preliminary form. Stone's classes do not include bar or edge detectors like those reported by Spinelli and neither Stone nor Spinelli include the uniformity detectors reported by Rodieck and Stone (1967). It thus appears likely that the proportion of non-concentric units reported in the cat retina will increase as the investigators improve their techniques. It is not conceivable, however, that any such increase would be sufficient to eliminate the difference between the two animals.

Consideration of the qualitative differences between the non-concentric units of rabbit and cat adds further evidence to the effect that the organisation of the visual system differs in the two cases. The rabbit visual streak contains five classes of non concentric unit, large field off, directional, orientation, local edge and uniformity detectors, all of which are considerably different in their properties from the concentric type. Most of the non-concentric units reported by Stone and Fabian in the cat are not much different from the concentric type. In this class fall the centre only, diffuse and on-off units which appear to form 94% of the non-concentric class. Directional, edge, bar and uniformity detectors are poorly represented and it does not appear likely that they will come to represent even the majority of the non-concentric class let alone all of it as in the rabbit.

At the time of Maturana's "deterministic-indeterministic" classification it appeared that the variety of retinal units decreased markedly with the development of neocortex in the mammals. Consideration of insect, amphibian and mammalian retinae suggested that the variety of retinal units might vary inversely with the volume of central tissue available for further analysis. The discovery that the rabbit possesses non-concentric units led to /

to the hypothesis (Hughes, 1966) that this mammal is an unusual case in that it possesses only a small amount of neocortex to deal with each element of its extensive area centralis. Its survival might thus be facilitated by the presence of a variety of units at retinal level; the advantages being analogous to those in frog or pigeon whose retina projects almost entirely to the tectum. The limited amount of cortex available for visual processing would be freed for other visual tasks and some compensation for the compressed visual streak representation would be effected. The more varied retinal analysis could provide a basis for understanding the retention of the high ganglion cell density along the streak in the absence of an extensive cortical representation.

The discovery of non-concentric units in the cat might be regarded as ousting the rabbit from its special position but the above comparison of rabbit and cat retinal units suggests that the populations differ sufficiently for the hypothesis concerning the uniqueness of the rabbit retinal organisation to be allowed to stand in a somewhat qualified form. It may be, however, that the variety of retinal units in the rabbit is a universal characteristic of the lower mammals and not a special adaptation to compensate for compressed cortical representation. It has recently been reported by Michael (1968) that the retina of the ground squirrel contains a single unit population as varied as, and similar to, that of the rabbit. The ground squirrel possesses an all-cone retina which is of uniformly high acuity and lacks an area centralis. The whole retina may thus be regarded as a form of 'visual streak' so that the animal may possess as compressed cortical representation of the visual field elements as the rabbit and a similar explanation for the presence of the non-concentric units may apply. At present the rat is the only other small animal from which evidence is available and in this case (Brown & Major, 1965) it appears that the retina does not possess a variety of units but these results have not been confirmed. The absence of variety lends weight to the above hypothesis; non-concentric units do not appear to be universal amongst the lower species.

A CRITIQUE OF CERTAIN COMMON IDEAS ABOUT RETINAL FUNCTION

The presence of non-concentric units in frog and rabbit retinae has led many students of vision to group the two animals together and to contrast them with the cat and monkey. Thus, after comparing the retinal units of the rabbit with the cortical units of the cat, De Valois (1966) goes on to say:

"It may appear strange that the higher animals take longer to do a certain type of data processing than do the more primitive frog and rabbit."

The rabbit has tended to be regarded as a member of the determinate class of visual systems as defined by Maturana (1964) but expanded to include appropriate mammals.

The finding of a significant proportion of non-concentric units in the cat has eliminated the distinction which had been drawn between the rabbit and cat on the basis of the erroneous assumption that the cat did not possess any non-concentric units whatsoever. On the other hand, as has been shown above, the smaller proportion and qualitative properties of the cat non-concentric units provide an alternative basis for the belief that the visual systems of rabbit and cat are differently organised at the retinal level.

Maturana's two classes of visual system - the deterministic and indeterministic - appear, subsequent to these findings in the cat, to have been replaced in the minds of workers in the field by a continuous scale. The relative positions of the species which have so far been studied are allocated according to the proportion of concentric units to be found in their retinae. In the absence of other criteria such a classification is natural but it unfortunately carries over a number of unjustified assumptions which have been generally accepted and which are specifically mentioned in Maturana's paper (1964). These assumptions are dealt with in the subsequent sections but may be listed as follows -

1. Concentric units are simple repeaters of the retinal image.
2. /

2. Ambiguity of response of a concentric unit is greater than that of a non-concentric unit.
3. There is some fundamental difference in the retinal organisation of animals with and without non-concentric unit.
4. Non-concentric units mean that the higher levels of the visual pathways are rigidly organised but economical of cells.

IS THE CONCENTRIC UNIT A SIMPLE REPEATER?

Certain statements and implicit assumptions which appear in the literature clearly suggest that the early classification of visual systems into determinate and indeterminate types partly arose from the idea that there is a considerable difference in the extent of information processing which is carried out by concentric and non-concentric units. Thus we have:

"The interpretation of the visual image in the frog begins at least at the level of the ganglion cells. But this is not a specific case. The same occurs in birds and reptiles."

In context Maturana (1964) thus implies that the interpretation of the retinal image does not begin in the cat until the level of the visual cortex. This attitude is apparent in the current literature and stems from the assumption that the concentric units act solely to convey a punctate representation of the retinal image to the central nervous system. Thus we find:

"If the retina of 'higher' mammals is simply a mosaic of 'on' centre and 'off' centre transducers ..."

"The evidence suggests that the retina of the cat is not a simple repeater, but that the coding of visual information is performed at least in part at this level."

In both quotations Spinelli (1967) is assuming that a retina containing concentric /

concentric units alone is a 'simple repeater' but that a retina bearing non-concentric units is not. Such assumptions are quite incorrect; there is no reason to assume that the concentric unit is a 'simple repeater'.

Consider the processing of the retinal image information before it reaches the optic nerve. The image is transformed into an electrical signal proportional to the log of the incident light flux at the photo-receptor inner segment. The whole image is thus turned into a mosaic of potentials and the spatial resolution possible at this stage is determined by the receptor outer segment size and spacing. In animals with colour vision the resolution is reduced because the receptors are of four varieties whose outputs do not mix until later stages. The presence of a red receptor at one point precludes sampling of that region of the image by a rod or by a green or blue receptor. Further potential spatial resolution is surrendered when the receptor outputs are summed in most parts of the retina in order to achieve greater sensitivity, i.e. spatial information is exchanged for greater sensitivity. At the level of the concentric ganglion cell itself, the information about the absolute level of illumination is abandoned (or this is usually accepted to have occurred) so that only differential stimulation of the centre and surround regions elicit a discharge. The elimination of a certain amount of spatial resolution at the receptor-bipolar junction results in the inability of the unit to signal the tangential movement of a spot of light if its excursions are small and limited to either centre or surround alone (Rodieck & Stone, 1965). Under these conditions a response is only obtained when the spot moves centrifugally or centripetally over regions of varying sensitivity. The reciprocal inhibition between the two regions of the concentric receptive field is usually regarded as preventing the response of the unit when its receptive field is centred upon a portion of the retinal image which lacks contrast. An image transformed by a matrix of such units loses little information of biological significance but is considerably reduced in redundancy (Barlow, 1961). The above considerations should make it clear that the concentric unit /

unit cannot be regarded as a mechanism for repeating the brightness at a point in the retinal image. It is probably best to regard such units as contrast detectors, at least under conditions of photopic illumination, if a name must be given although the following facts indicate that their function is not so straightforward as is implied by the idealised account found in many publications.

The original paper of Kuffler (1953) and the work of Rodieck and Stone (1965) make it clear that the concentric units of the cat retina differ considerably in the extent of the reciprocal interaction of surround and centre. Nearly all ganglion cells give a response to the flashing of diffuse background illumination covering the whole receptive field. Some give a response of the centre phase and others of the surround but this is a function of the background intensity and changes for a given unit with the ambient conditions. The extent and variability of the response to diffuse light are not what would be expected to be required for operation as a contrast detector. The response pattern to flashes of diffuse or restricted receptive field illumination is not, however, related to the effect of illumination on the maintained firing (Rodieck, 1967). On and off centre units may show either an increase or a decrease in firing rate upon changing from dark to light. No consistent relationship between unit type and maintained firing has been observed although some units do show the type of relationship that might be expected. Such units probably account for reports of cells firing at rates proportional to the illumination intensity; the flux detectors of Spinelli and Weingarten (1966). The division of the centre on and centre off units into two major classes depending upon the linearity of summation of light intensity throughout the receptive field (Enroth, Kugel & Robson, 1966) may, in due course, offer a basis for resolving the confusing variety of responses which are available from apparently only one class of unit.

Barlow (1965) has suggested that the centre surround arrangement exists in order to achieve high sensitivity to small changes in light intensity /

intensity over the whole of the 10^{10} fold range of intensities met in the photopic environment. Under the whole range of possible photopic background conditions the centre and surround responses cancel out almost completely leaving the range of firing frequencies available for coding the response to differential illumination with a high quantum/spike ratio (high sensitivity). A unit without a surround would be capable of coding only a tiny fraction of the whole range if it were to possess similar contrast sensitivity.

The coding operation of the concentric units thus appears to involve unexpectedly complicated processes and still remains unclear. A further rather baffling problem exists in the absence of an explanation for the presence of two classes of units, the centre on and centre off types, which possess apparently complementary properties. The majority of these units has a maintained discharge which is capable of increasing or decreasing with sinusoidal light intensity variations over a range of frequencies (Hughes & Maffei, 1966). In view of this it might not appear likely that the off units exist to signal darkening and the on to signal brightening (Jung, 1961) because either population is capable of that on its own. It is clear, however, that separate on and off systems may be required because firing suitable to act as a carrier tends to disappear at higher levels of the nervous system.

SPECIFICITY OF RETINAL UNIT RESPONSE

One of the more frequently emphasised characteristics of the concentric units is the greater ambiguity of their response when compared with the non-concentric units. Maturana says of the cat concentric units (1964),

"... the retinal ganglion cells of the cat respond in the same manner to a variety of stimuli.... The meaning of the activity of the retinal ganglion cells of the cat is then ambiguous and unspecific. It is not possible to tell what happens in the visual field by looking at the output of one ganglion cell only."

In /

In the previous section, however, we have seen that the concentric unit is not a 'repeater' and, like the non-concentric unit, is restricted in a number of ways in the range of information that it can pass on to the CNS. Thus having already inverted the usual procedure by considering not the ambiguity but the specificity of the concentric unit let us take note of the ambiguity rather than the specificity of the non-concentric units.

Two classes of specialised unit possessing ambiguous response patterns immediately come to mind, the uniformity detectors and the large field off units of the rabbit retina. The former responds to almost any visual stimulus by inhibition of a maintained discharge while the latter gives a response to a variety of shadow and flicker stimuli. In both of these cases the ambiguity of response is rather greater than in the case of a standard concentric unit such as may be recorded in rabbit or cat retina.

The edge orientation receptor of the rabbit retina will respond to the on, off or on-off of a light spot depending upon where it is placed in the receptive field. The movement of objects through the receptive field in various directions will give rise to a response if they are no larger than the field size. Stationary or moving stimuli are adequate to elicit a response. In a sense the unit may be regarded as more ambiguous than those concentric types which possess an active surround because it will respond to one set of orientations of stimuli which extend across the on and off receptive field while many concentric units will not respond well or at all to such a stimulus if centre and surround are simultaneously activated.

As a final example we may consider the directional units of the rabbit retina. These cells will fire in response to the slow movement of a stimulus in the null direction across the receptive field or to the flashing of a light spot on and off within the movement sensitive region. If the unit does not fire, it is possible that a stimulus is present in the receptive field but moving in the null direction or that nothing is present. Movement through the receptive field in directions other than the null may elicit firing which is influenced by the velocity of movements of the stimulus /

stimulus, its brightness and its course through the receptive field.

It would clearly be mistaken, on the basis of present information, to maintain the assumption that non-concentric units are more rigidly organised with respect to the information they can transmit than are the concentric types although, of course, their transmission characteristics are clearly different. Similar considerations apply to the frog retinal units which are more ambiguous and not so invariant in response as Maturana et al. (1959) suggest (Keating personal communication) and which will respond in most cases to light flashes of stationary spots as well as to the more commonly emphasised moving stimuli.

The excessive insistence on the functional specificity of the retinal non-concentric units which is displayed in the literature may stem in part from the system of unit class nomenclature. As long as the names given by various workers to different classes of unit are used simply as a label while the actual behaviour of the unit type is determined by a close perusal of the original paper, then no problem exists. Certain authors and many readers do not use the nomenclature in this fashion. Thus Maturana et al. (1959) sought to determine the particular quality of the normal visual environment of the frog which elicits the greatest response from each class of retinal units. Each unit type was labelled as a detector of one such specific quality. Such properties of the visual environment have been called 'trigger features' by Barlow et al. (1964). The assumption that trigger features once determined may be equated with the natural stimuli detected by the unit considered may lead to difficulties but these will be discussed in the next section. For the moment it suffices to consider one case of the search for a trigger stimulus leading to the neglect of other forms of response from the unit.

The orientation selective units of Levick (1967), horizontal and vertical edge detectors of Maturana (1964) and the on-off adjacent units of Hughes (1966) all appear to possess similar properties. Of such units Maturana (1964) said

"The /

"The output of these cells can mean only one thing for each: a vertical and a horizontal edge respectively."

If, as appears likely, the units in the pigeon operate by a similar mechanism to those in the rabbit optic nerve, the the above statement is not valid; the units may equally well be described as 'axial motion detectors'. The movement of any object along the axis connecting the centre of the on and the off fields will usually evoke firing in both directions but movement at right angles to this along the overlapping region of the field components produces no response. The tendency to seek 'trigger features' is unfortunately so ingrained that one's immediate response to this information is to consider whether the unit acts in the natural state as either an axial movement detector or as an orientation detector and to neglect the possibility that some more general function may be revealed. The need for a short and convenient classificatory term for the various types of unit thus inevitably leads to the ignoring of other features of the response. In view of this it would appear best to use non committal descriptive terms such as on-off adjacent unit, large field off unit rather than the more attractive 'orientation detector' or 'alarm unit'.

UNIVERSAL RETINAL ORGANISATION?

In 1961 Lettvin et al. attempted to equate their five classes of frog optic nerve unit with five types of ganglion cell dendritic tree observed in the drawings of Golgi preparations of frog retina made by Ramon y Cajal (1894). Some of the cells were found to possess dendritic trees which ramified in more than one stratum of the inner plexiform layer. Such cells were described as multistratified.

A similar correlation was attempted by Brown (1965) between the dendritic trees of methylene blue stained ganglion cells in the rat retina and two classes of optic nerve unit observed by Brown and Rojas (1965) in the same animal. It appears to have been assumed by Brown that the presence of multistratified cells in the frog is associated with the variety and complexity /

complexity of the stimuli required in order to obtain a good response from frog retinal units for we find the following statement (Brown, 1965):

"No multilayered ganglion cell dendritic trees were found in the rat retina; hence no receptive field organisations as complex as those of the frog are to be expected, nor were they discovered physiologically."

Brown's assumption is further indicated by his comment that Polyak (1941) did not report multilayered ganglion cells in the monkey retina which also appears to possess only concentric units.

My own failure to observe the presence of multistratified ganglion cells in the rabbit is confirmed by a comment, based on unpublished work, by Brown and Major (1966). The absence of such cells in the rabbit, which possesses a greater variety of single unit fields than the frog at the retinal level, shows the inadequacy of the structure function relationship assumed by Brown. Recent evidence (Gaze & Keating, personal communication) suggests that even the structure-function correlation suggested by Lettvin et al. (1961) is inadequate. The significance of the multistratified cell remains a mystery but it is certainly not related to whether a retina bearing it contains concentric or non-concentric units.

Hubel and Wiesel once stated (1962):

"Perhaps even more surprising, in view of what seem to be profound physiological differences, is the superficial anatomical similarity of retinas in the cat and frog. It is possible that with Golgi methods a comparison of the connections between cells in the two animals may help us in understanding the physiology of both structures."

The greater similarity between the rabbit and cat, rather than cat and frog, retinas might be regarded as more surprising in view of the difference in the properties of their single unit populations. Since the paper by Brown (1965) there has been no suggestion of anatomical differences which may be correlated with differences in the unit populations of the retinas of different /

different species. It may not, however, be realised that the mechanisms ^{of} ~~showing~~ the characteristic responses of the common classes of the retinal unit can be shown to be, or explained as, the result of the operation of similar processes in the case of concentric and non-concentric receptive fields. The unifying principle appears to be the use of differentially distributed spatial inhibition.

The possibility of demonstrating the relationship between the concentric and non-concentric units arose from the work of Wagner, McNichol and Wolbarsht (1963). While recording from goldfish retinal concentric units, whose centre and surround possess different spectral sensitivities they were able to demonstrate, by the use of appropriate wavelengths for the light stimulus, that the surround response could be elicited from any part of the centre and the centre response from much of the surround. The characteristic on or off centre concentric map was obtained, however, when white light was used as a stimulus. The appearance of the concentric field thus appears to arise as the result of the simultaneous stimulation of overlapping on and off regions and the nature of the response from a given point depends upon the relative sensitivity of the two concentrically arranged receptive regions at that point. Rather different methods have been used by Rodieck and Stone, (1965) and Enroth-Kugell and Robson (1967) who have independently established that this concept of receptive field organisation is applicable in the case of cat units where the possibility of using differential spectral sensitivity to demonstrate the similarity of organisation to goldfish units does not exist.

It will be immediately apparent that the displacement of the on and off components a concentric receptive field while they retained the same connections to the ganglion cell, would convert the unit into an on-off adjacent type, or edge detector. An examination of the properties of such a unit, as shown in fig. 52, reveals the identity of the reciprocal interaction between the on and off regions to that observed in the concentric units.

The /

The uniformity detector requires no more than the arrangement of concentric on and off areas feeding inhibition on to a spontaneously active ganglion cell. These units are the 'suppressed-by-stimulus' type reported in the cat by Rodieck (1967).

The centre only and diffuse units of the cat and the large field off units of the rabbit are similar in organisation to the concentric type and do not require the postulation of any basically new mechanism.

The on-off units of the rabbit, directional and edge detectors (contrast or amount of edge detectors), are not so straightforwardly related to the concentric type in organisation. The directional unit is clearly obtained, however, by the use of a selectively distributed inhibition and reasons have been given (p. 67) for the assumption that this process is carried out in the inner plexiform layer and may involve amacrine cells similar to those invoked for the explanation of concentric unit function (Boycott & Dowling, 1966). The edge detectors have been suggested to involve similar mechanisms to the directional unit (Levick, 1967).

It would thus appear that the difference between retinae possessing units with a variety of physiological properties may ultimately be detected anatomically only if it becomes possible to specify the functional nature of specific interconnections between cells.

CONCLUSION

Consideration of the properties of various types of visual system led Barlow (1961b) to suggest the possibility of two types of sensory relay (retinal) organisation:

1. Detects, in the incoming messages, certain 'passwords' that have a particular key significance to the animal.
2. Recodes sensory messages, extracting signals of high relative entropy from the highly redundant sensory input.

These two classes correspond, in part, to Maturana's concept of determinate and indeterminate organisation but are not mutually exclusive nor are they tied to the presence of any particular retinal unit type or group of animals.
At /

At present, however, it is not possible to decide whether, or the extent to which, each process is carried out in any given animal. The nature of retinal coding is not understood and no behavioural response has been shown to originate in the activity of a certain specific class of specialised retinal units. The idea is, however, useful for it emphasises the importance of understanding the central functions of the unit types. The validity of Barlow's hypothesis cannot be tested by analysis of the visual units at retinal level alone. Thus, although it is of interest that the frog might be regarded as the possessor of a class 1 'key feature' detecting visual system (Barlow, 1961), there has been no demonstration that the so-called fly detector units play such a role in life. It is perhaps advisable to note that the rabbit, which has a very different diet to the frog, possesses a goodly population of streak units which have properties nearly identical to the frog fly detectors.

One of the more puzzling aspects of the comparative study of single unit populations is that the animals so far examined do not either possess all concentric units or all non-concentric units but may be arranged in a series ranging from the frog, which does not have any standard concentric units, to the monkey, which apparently has concentric units alone, but including animals in intermediate conditions such as the rabbit and cat in which the concentric units form 35% and 75% of the total populations respectively. In the following series of animals the percentage of concentric units increases and the variety of the population decreases in moving from left to right:

frog - rabbit - cat - monkey.

Examination of the above series reveals that it is the same as that which may be obtained if the animals concerned are arranged in order of the ratio Visual cortex area / Superior colliculus area:

frog	rabbit	cat	monkey
0	1.5	9.0	30.0

This series provides a ready basis for the combination of Barlow's concept of a twofold sensory relay function with the range of populations of unit types /

types to be found in various species. The non-concentric units might be regarded as projecting to the superior colliculus where their 'key feature' detecting properties could be employed in the initiation of certain specific responses related to collicular function. The concentric units might be regarded as projecting solely to the visual cortex where they could provide the basis for a more general analysis of the visual environment. Such an arrangement would mean that the retinal unit population would reflect the extent of cortical dominance within the visual system of the animal. It is unfortunate that the limited evidence available appears to contradict this straightforward hypothesis. In the rabbit it is clear that the visual cortex receives a variety of non-concentric projections from the retina while in the cat some non-concentric units, which are presumably of retinal origin, are found in the LGN where they will be en route for the cortex (Kozak et al., 1964).

None but the most optimistic speculator would now expect the properties of the retinal units to reveal per se their role in the normal animal. We must consider the units in the context of evidence of their central function.

Retinal function has often been compared to a filtering operation such as is carried out in many engineering systems. The high selectivity of transmission possible in such systems may influence the physiologist to regard the ambiguity of retinal unit response as an inadequacy of retinal organisation which may therefore be suppressed in the search for a clear classification of the unit types. In fact, such ambiguity may be of central importance. It has been pointed out that the range of our colour vision is dependent upon the broad band spectral sensitivity curves of the receptors. This ambiguity of response is an asset but under other circumstances it is clear that the CNS is capable of interpreting such apparently ambiguous inputs in order to generate a specific output. Thus /

Thus the crustacean optomotor response is elicited by movement alone in spite of the fact that movement detector units will respond to a variety of stationary stimuli (Horridge, 1965).

There are certain cases of units for which it is possible to make a guess at natural function. The large field off unit of the rabbit retina has been shown to project to the superior colliculus (Hughes, 1968; see subsequent section) where it is very likely that it plays the part of an 'alarm unit' and may be involved in the generation of the orientation reflex. The directional unit of the rabbit retina has been a most puzzling type. The term 'directional unit' would suggest that the unit fires in response to the movement of an object through its field in one direction and not in any other. In actual fact the directional unit fires in response to movement into the field over an arc of about 300° and not at all in response to movement in over a restricted 60° arc. A response to a moving object conveys little information about its direction of motion while the absence of a response may mean that something is moving through the field in the null direction or that nothing is moving at all. It is clear that such ambiguities could be resolved by simultaneous consideration of activity in a variety of units but then the advantage of such a 'key feature' selector is less apparent; a collection of concentric units would suffice. The discovery that the directional units fall into four groups each arranged so that the preferred direction of firing coincides with the direction of pull of one of the four eye muscles (Barlow & Oyster, 1967) reveals how, without further central processing, the output of the units could serve as an error signal to minimise retinal image motion. If the retinal image moves, the directional units fire and cause a contraction of the appropriate eye muscle, or muscles, to oppose the image motion; if the contraction is excessive, the image motion will reverse and pass in the null direction through the receptive fields of that class of directional units thus inhibiting their firing. These units would thus be envisaged as playing a role in field fixation reflexes rather than as applying information about the movement of specific /

specific objects in the visual field as had previously been thought.

Unfortunately such clues are not available to aid understanding of the role of other classes of retinal unit. A classic example of relying upon a stimulus orientated classification for the determination of functional role is the christening of the class 2 unit of the frog as a 'convexity detector' (Maturana et al., 1959). The error has been pointed out by Gaze and Jacobson (1963). The greater response to small objects (tending to possess greater convexity than large objects) simply results from the presence of an inhibitory surround. As Barlow^{et al} (1964) say, while falling into a similar error:

"The response has nothing to do with 'convexity' as such: frogs are interested in flies, not in the mathematical abstractions that preoccupied the investigators."

In arguing against Maturana's concept of determinate and indeterminate visual systems the idea has been developed that the information transmitting capabilities of the concentric and non-concentric units are not to be regarded as necessarily different in magnitude. Neither class of unit should, in the absence of a considerable advance in the quantitative theoretical aspects of the subject, be regarded as more ambiguous, economic or rigid in capability than the other. The evidence available shows that there is a greater variety of retinal analysis in some animals than in others but this should not be equated with a greater amount of preanalysis. Like Barlow, we emphasise the importance of the operations carried out at a suprarretinal level for the determination of the flexibility of visual behaviour. Unlike Maturana, we do not regard retinal selectivity as the limiting factor in this respect. The recent observations of Grusser, Finkelstein and Grusser-Cornehlis (1968) supports this view in indicating the considerable ambiguity of the retinal response of frog units.

"From this observation it is evident that in the different classes of retinal neurons no 'functional natural invariants' are formed out of /

of the set of possible natural stimuli as was assumed by Maturana, Lettvin et al."

It has already been suggested that the compressed cortical representation of the visual field in the rabbit is to some extent compensated for by the use of a more varied analysis of the image at the retinal level. This suggestion may be understood as similar to that of Arden (1963) which implies that the rabbit carries out, at retinal levels, operations which are dealt with at the cortical level in the cat.

"It may be that similar functional organisation occurs in the visual system of all vertebrates, but the less encephalised the animal, the lower the level in the chain of sensory neurones at which sophisticated analyses of the incoming information are made."

There is little evidence to suggest, however, that the rabbit retinal units do perform equivalent functions to those of the cortex in the cat. An obvious case is that of the orientation detector of the rabbit retina and the oriented bar detector of cat cortex. The former is found in either of two orientations, the latter in about 20. These units could be involved in the role of orientation detection in cat cortex but are not adequate for such a role in the rabbit retina. Van Hof has found that the rabbit is readily trained to distinguish between a 45° grid and one with either horizontal or vertical bars (1966). It is also capable of detecting rotations of such grids through less than 6° . It is clear that the rabbit uses some information other than that from the on-off adjacent units in this task.

A subsequent section will discuss the problems of comparing rabbit, cat and monkey visual cortex organisation but sufficient information on rabbit cortical units has been presented, page 138, to indicate that their properties are very different to those in cat and monkey. This must not be taken to mean that the rabbit system is organised to detect a limited repertoire of 'key features' or is of lesser information processing capacity. The presently available information indicates no more than that there is an apparently major difference between the operations of the visual pathways in rabbit and cat.

STRUCTURE AND FUNCTION IN THE RETINA

In "Receptors and Sensory Perception" (1955) Granit wrote:

"...even if there are simpler structures than the retina available for the study of synaptic excitation and inhibition, the understanding of the principles of central organisation and transmission of sensory information is never likely to be very much in advance of our understanding of the principles governing the form and delivery of retinal messages."

Many arguments can be put forward for the use of the retina, once described as a "brain on a stalk", as a paradigm of the central nervous system. At present the advantages of the retina for comparison of structure and function in nervous tissue may be tabled as follows:

1. The retina contains only five classes of neuron; receptor, horizontal cell, bipolar, amacrine and ganglion cell.
2. The perikarya of these cells are arranged in three separate layers.
3. Synaptic contacts between the cells are limited to two layers to each of which only three types of neuron contribute.
4. The predominant direction of information flow through the retina is from the photoreceptors to the ganglion cells which considerably aids the interpretation of function.
5. The retina is subject to very little control by other regions of the nervous system and the photoreceptor matrix is almost its entire input. The anatomical lamination of the retina is especially favourable to the use of the electron microscope for the elucidation of the interconnections between the limited variety of cells and should also facilitate the correlation of histology and physiology.

In spite of these assets, however, the analysis of retinal function is not proving easy. Until recently only the output of the ganglion cells had been directly examined but, as yet, nobody has unequivocally established their ability to record from the horizontal, bipolar and amacrine cells and to establish their functional properties. It was as late as 1965 (Tomita, 1965) that records were made of individual photoreceptor activity and much remains /

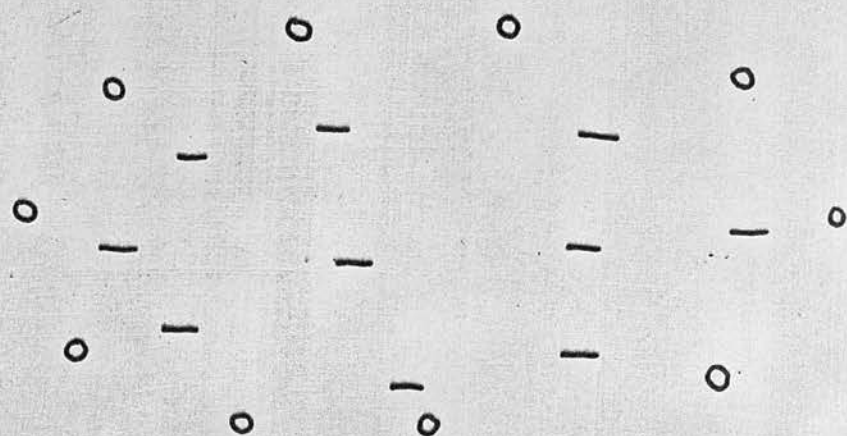
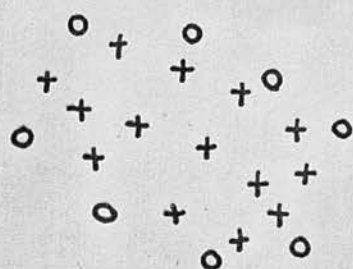
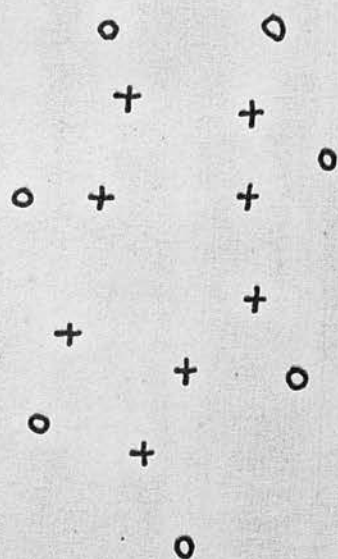
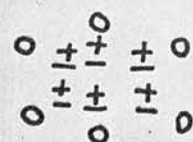
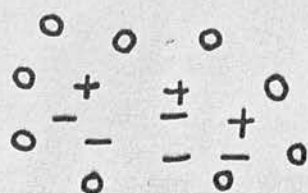
remains to be found out about these cells. It is possible to use the available data to make some guesses about the properties of the cells in the inner nuclear layer but before becoming involved in that activity let us consider the little that is known about structure and function of the receptive field of retinal ganglion cell units.

STRUCTURAL BASIS OF CONCENTRIC RECEPTIVE FIELD

Centre. In 1966 Brown and Major suggested that the size of a concentric unit receptive field centre is determined by the diameter of its ganglion cell's dendritic tree. According to Wiesel (1960) the total receptive field size, including centre and surround, is usually 2-3 mm. in diameter in cat retina and is never smaller than 1.5 mm. The dendritic trees of retinal ganglion cells outside the area centralis were reported by Brown and Major as possessing diameters from 70 to 700 μ which indicates that they alone cannot account for the size of the total receptive field. Wiesel and Rodieck and Stone (1965) both note, however, that the diameter of the receptive field centre varies from 110 to 880 μ in passing from the pericentralis area to surround. Brown and Major held that the range of centre diameters measured by Rodieck and Stone (1965) coincided quite well with the range of dendritic tree diameters measured by ~~them~~^{Wiesel}. The bipolar dendritic trees are in the order of 30 μ in diameter and would thus add to increase the physiologically determined receptive field of a ganglion cell to a diameter in excess of its dendritic spread. It should also be noted that no account was taken of shrinkage in the retinal preparation so that the measurements of dendritic spreads should perhaps be increased by about 10-15% which would bring them more into line with the physiologically determined receptive fields.

This work was reinvestigated by Leicester and Stone (1967) and found to be valid for the cells outside the area centralis. There is, however, a more considerable divergence of the anatomical and physiological results within the area centralis. The receptive fields of the region are reported /

Fig. 107 Oval receptive fields of the optic nerve units drawn to the same scale as the dendritic tree diagrams of fig. 25.



reported (Stone and Fabian, 1966) to be of centre diameter from 85 to 110 μ while the dendritic tree spreads are in many cases less than 15 μ . It is, however, possible that either the smallest receptive fields have not yet been examined or that the dendritic trees in the area centralis are not properly stained. My own experience of cells in the rabbit area centralis suggests that the latter may well be the case.

There is general agreement that Brown and Major's suggestion is valid in the case of cat concentric units. The only other animal for which adequate data is available is the rat. It is possible to use the data of Brown (1965) on rat concentric units to show that the range of field centre diameters, 170-570 μ , corresponds well with the range of dendritic tree spreads, 200-600 μ .

The receptive fields of the rabbit are of too varied function for such a correlation to be attempted although it is clear that the range of ganglion cell field diameters corresponds well with the receptive field diameters in this animal. A different correlation of receptive field and ganglion cell dendritic tree organisation has, however, been observed in the rabbit retina. The receptive fields of single units in retina (Barlow, 1964; Levick, 1967), LGN (Arden, 1963) optic nerve and cortex (my own observations) have often been noted to be oval in shape with the long axis arranged parallel to the horizontal. Figure 107 shows the receptive field maps of a number of optic nerve and retinal units drawn to the same scale as the dendritic trees of fig. 25. The ratio of the major to the minor axis is found to average 2:1 in the case of receptive field and ganglion cell dendritic trees.

The receptive fields of units situated at the end of the band of myelinated fibres would be predicted to have the long axis vertical if it is determined by the shape of the ganglion cell dendritic tree. An examination of the field plots of recorded optic nerve units revealed three such units but in no case had the position of their projection on to the retina been noted. A number of fields orientated with the long axis at intermediate angles /

angles were also noted as might be predicted from the orientation of ganglion cell dendritic trees. These features of the optic nerve receptive fields were not observed until the experimental series had been discontinued so there has been no opportunity for a more comprehensive examination to be carried out.

It has previously been suggested that there are good reasons (p. 196) to expect the failure of the more ambitious attempts to correlate overt ganglion cell structure with the functional type of receptive fields. So far only two attempts at such a feat have been made. The first, by Maturana, Lettvin, McCulloch and Pitts (1964), was carried out for frog units but clearly had no quantitative basis and has not subsequently been confirmed. In the second, Brown (1965) was unable to find any clear relationship between the receptive field organisation and dendritic trees of the rat retina. No structural basis for differentiation between on and off centre fields has been observed.

The surround. If the concentric unit receptive field centre is represented by the ganglion cell dendritic tree spread then we are left with the problem of which cells are involved in the generation of the surround region of the field. A critical examination of the literature reveals that none of the presently available hypotheses concerning the structural basis of the surround are well founded and later parts of this section are directed to the presentation of the facts which must be assimilated in any successful hypothesis rather than with propounding such a hypothesis.

There is certainly good reason to regard the functional basis of the surround as different from that of the centre. In addition to the anatomical information presented above there are two important physiological indications. The first, Barlow, Fitzhugh and Kuffler (1957), is that the surround of a concentric unit ^Pdisappears upon prolonged dark adaptation leaving the centre region functioning normally. The second is that the latency of the response from the surround is longer than that from the centre in concentric units (Barlow, Hill & Levick, 1964). This latter effect is not /

not the result of weakness of the surround response because the effect is found when the centre response is less marked than that of the surround.

The region of receptive field from which on, off or on-off responses can be obtained in directional and on-off adjacent units etc. is usually regarded as equivalent to the centre region of the centre surround units in that its extent is determined by the ganglion cell dendritic tree although no such correlation has yet been demonstrated. Two points indirectly support this view. It has been observed by Barlow et al. (1964) that the latency to on and to off responses in the directional units is similar in both cases and invariant with position in the receptive field. Secondly, many of the non-concentric unit types possess a surround region with only the property of inhibiting the response of the centre. This surround may be of similar origins to the surround of the concentric units.

Hartline (1938) described the receptive field as the region of retina from which stimulation with light spots elicits activation of the retinal neurons. The possibility of a centre-surround organisation of the receptive field was first discovered by Kuffler (1953) in the cat. Although centre and surround are mutually inhibitory they are each capable of eliciting a response from a unit when stimulated. The term excitatory receptive field (E.R.F.) was adopted by Grusser, Grusser-Cornehlis and Bullock (1963) for such regions capable of initiating firing of a unit. Zones of the retina which simply inhibit the ganglion cell response but which are unable to activate the cell (Barlow, 1953; Barlow et al., 1964) were described as the inhibitory receptive field (I.R.F.).

The extent of the surround region of receptive fields is difficult to ascertain since the effect of a spot of light in an ERF tends to reduce rapidly with distance from the centre of the receptive fields. The most successful method is the area / threshold intensity measurement for a spot of light which is flashed at successively greater diameters. By this method the surrounds of the cat retina are found to extend no more than about 6° from the centre of the receptive field. The expanding spot test described /

described in an earlier section (p. 51) adds the stimulus of a moving edge to the general increase or decrease in illumination and by this means it is possible to demonstrate an ERF extending as much as 10° from the receptive field centre in certain rabbit retinal units (p. 55). The surround demonstrated by the expanding spot test may have somewhat different origins to that which may be elicited by flashing light spots. Certainly the units possessing large surrounds demonstrated by the expanding spot cannot be shown to possess such large surrounds when examined with flashes of very bright spots. Stationary annuli have not yet been used so it is impossible to say whether the efficacy of the expanding spot as a stimulus is dependant upon areal summation alone or whether the moving edge in some way lowers the threshold to light stimuli in the extreme periphery. For the present the surround demonstrated in this fashion will be assumed to be similar in properties and functional basis to that demonstrated by stationary light flashes.

The relationship to the ERF surround to the inhibitory surround of, say, cat 'centre' units and rabbit directional units is another matter unresolved at present. Most of the frog units possess such IRF regions in their receptive fields but no detailed study of their properties has been made. It would be of interest to subject fields demonstrating IRF regions to dark adaptation of prolonged duration. If the IRF region were to disappear, as does the surround of cat concentric units, then its mechanism might be assumed similar to that of an ERF surround region.

The problems relating to the surround region were increased in 1964 when McIlwain demonstrated the so called peripheral effect (P.E.) in which it was noted that the movement of a card stimulus, whose use eliminates light scatter, in the periphery of a unit at distances of some $30-40^\circ$ for the centre would increase the spontaneous firing rate of the unit or increase its tendency to fire when a threshold light spot is flashed in the centre or surround. The magnitude of the effect varied inversely as the distance from the centre of the receptive field and was very sensitive to the effect /

effect of anaesthetics. A variety of arguments indicate the retinal origin of the effect (Levick, Oyster & Davis, 1964) while the sensitivity to anaesthetics and the long latency of the effects onset after stimulation suggest the involvement of multisynaptic pathways. Such an arrangement seems inevitable since the dendritic spread of the largest retinal cells reported from any animal, the Marengi cells (Gallego & Cruz, 1965), is not adequate to account for the spread of the McIlwain peripheral effect. It is important to note that the PE acts on both centre and surround in excitatory fashion and thus cannot be regarded as an extension of the ERF-surround in the usual or extended form demonstrated by the expanding spot test.

Any adequate model of concentric unit organisation must account, at least, for the following physiological observations and should also provide a structural basis for them.

1. The retina contains on and off centre units which demonstrate a similar latency of response.
2. Centre and surround may, when appropriately stimulated, cause the ganglion cell to discharge.
3. On and off surrounds show longer latency of response than the centre regions.
4. After prolonged dark adaptation the surround organisation disappears but the centre region of the receptive field remains little changed.
5. Simultaneous stimulation of centre and surround in the same phase reveals inhibition of the centre response by the surround.
6. Simultaneous stimulation of the centre and surround in the same phase reveals inhibition of surround response by the centre.
7. Excitation of the ganglion cell from the surround by an appropriate light flash out of phase with another simultaneously applied to the centre which would normally elicit excitation reveals inhibition of centre from surround or competition between the two.
8. The centre may be shown to have a similar effect to that described in (7) on the surround.
9. /

9. Independent spatial summation of stimuli can be demonstrated throughout centre and surround.
10. Moving stimuli in the periphery can excite centre and surround up to distances of some 40° (P.E.).

Most of these conditions have been culled from Kuffler's 1952 and 1953 papers but the sources of the other points will be found in the preceding pages. No systematic investigation of centre surround organisation, other than Barlow et al.'s examination of dark adaptation (1957), has taken place since the work of Kuffler. No current hypothesis explains these facts.

One major problem is to account for the presence of an off ERF while, at the same time, including an explanation of the reciprocal inhibition which may be demonstrated between the centre and surround. The ideas of Wolbarsht, Wagner and MacNichol (1960) appear to have dominated in the models currently presented to account for these phenomena. These workers suggest that the ganglion cell excitation arising from an on region when a light is flashed occurs as a result of a straightforward depolarisation of the cell membrane. The inhibition of this response by the illumination of an off region is suggested as occurring as the result of a hyperpolarisation of the membrane which results from the presence of appropriate connections from the off area of the receptive field. The off response is described as an post-inhibitory rebound which arises in a similar fashion to the anode break phenomenon demonstrable in peripheral nerve (Hodgkin & Huxley, 1952). The inhibitory effect of the off region on the on excitatory region is thus explained by the same connections as the off discharge.

The explanation is not adequate for a number of reasons. The most important point arises when the spatial interaction of the regions is considered. Wolbarsht et al. (1960b) suggested that

"the simplest explanation for the observed character of the 'off-center' receptive field is that the central area consists of receptors which have an inhibitory influence on the ganglion cell and give 'off' responses while the periphery contains receptors which excite 'on' responses."

Such /

Such an arrangement will account for the inhibition of the surround response by the centre but provides no explanation for the inhibition of the centre off response by an off in the surround. In an on centre unit, the hypothesis fails to explain the inhibitory effect of an off in the centre region upon an off response elicited from the surround. In neither type of unit does the arrangement account for the conditions (7) and (8) according to which an off in an off-region and an on in an on-region will inhibit one another.

The hyperpolarisation theory of off responses may simplify the complexity of the postulates required in a model of concentric units but it is inadequate in that it fails to account for prolonged off response or for the maintained off responses which may be observed in many animals. Post hyperpolarisation sensitivity is a relatively short lasting phenomenon.

Both Dowling and Boycott (1966) and Rodieck (1967) have used the inhibitory synapse as the basis for generating off effects in their models of concentric unit organisation and their systems consequently are subject to the same criticisms that are applicable to the model of Wagner et al. (1960). In that Dowling and Boycott (1966) attempt to account for a number of other conditions specified in the above list it is worth making a further consideration of their suggestions.

The paper of Wagner et al. (1964a) predated Brown and Major's (1966) demonstration that the center region of the concentric unit appears to correspond in size with the distribution of the ganglion cell dendritic tree. Wagner et al. clearly thought in terms of the bipolars at the periphery of the ganglion cell tree acting as a surround. Dowling and Boycott (1966) introduced the suggestion that the surround originates in the amacrine layer which acts on the ganglion cell by connections to the ganglion cell dendritic tree. The action of the amacrine upon the ganglion cell was suggested to be either inhibitory or excitatory depending upon the type of unit considered and the theory thus faced the same problems as those mentioned in relation to Wagner et al.'s model. The use of the amacrine as the region contributing the surround to the ganglion cell accounted for the longer latency of the /

the surround response, the presence of overlapping centre and surround fields both continuous through the receptive field, the possibility for independent disappearance of the surround region in dark adaptation and the presence in some units of surrounds extending further from the receptive field centre than any common retinal cell could account for. The amacrine cells of a number of species have been observed to possess lateral synaptic connections which would enable stimuli to have widespread effects by passage from one cell to another.

The amacrine spread, lateral synaptic interconnections and projection to ganglion cells is suggested in the Dowling and Boycott paper as a basis for the MacIlwain effect as well as for the normal concentric surround. The description of the MacIlwain effect in their paper is, however, rather vague

"... the periphery of a receptive field in a cat retina may extend considerably further than earlier work had suggested. In fact effects on ganglion cell discharge could be demonstrated upon stimulation 1.0 mm. or so from the receptive field centre".

It is not indicated that the peripheral effect of MacIlwain consists of an excitation of centre and surround which cannot be regarded as simple extension of the concentric ERF surround or as originating in the same retinal system.

The idea that the amacrine cells form the basis of the concentric surround response is thus attractive but only supported indirectly. The horizontal cells also extend their processes laterally in the retina but are excluded as a possible basis for the surround by Dowling and Boycott because the individual cells are not large and no lateral synaptic connections had been observed between those of the primate, whose retina their paper deals with. Such connections may, however, be present in the primates but so far unobserved because they have been seen in cat and rabbit (Dowling, Brown and Major, 1966) and in teleost fishes (Stell, 1966).

It would clearly be possible to go on to consider the anatomical pathways /

pathways available in the retina and to develop a number of alternative models of retinal function. By this method a block diagram of necessary events in the retina might be drawn up but these could be manifested in a great variety of ways. There are too many interactions in the retina in which the properties of the contributing cells are not known for such an approach to narrow down the number of possible retinal organisations to a reasonable figure. Too many alternative systems result and too many assumptions are required. We require more data on the cells of the inner nuclear layer before indulging in such speculative activities.

Brown and Wiesel (1959) made recordings of units in the inner nuclear layer and found a centre surround organisation like that of ganglion cells. It has been suggested that the recorded units were displaced ganglion cells but the work has not been confirmed or contradicted in the literature. Very extensive schemes of retinal organisation have been published by Svaetichin and his group but these have been subject to annual revision and are not seriously entertained. It is typical of the literature on the inner nuclear layer that Mitarai claimed to localise the S potential to horizontal cells or amacrine cells in 1958, in 1960 this was changed to the bipolar cells while in 1961 the various components were described as being located in horizontal, Müller and amacrine cells. At present the literature on the retina distal to ganglion cells is confused and as the matter does not lead anywhere it will not be discussed in this work. The interested reader is referred to the excellent review of this topic in the thesis of Stell (1966).

The recent intracellular records made from cones of the goldfish retina open up the possibility of extending the techniques to the recording of other retinal components (Tomita, 1965; Tomita, Kaneko, Murakami & Pautler, 1967). The records have clearly been established as from the cone inner segment (Kaneko & Hashimoto, 1967) and to come from three types of cone with different spectral sensitivities. Although all receptors so far recorded give a hyperpolarising response to the onset of light, it will be realised that /

that this event is recorded some distance from the pedicle. We thus still do not know whether the receptors are all of an on type or whether off types are present, whether pedicles are excitatory or inhibitory in their action and so on. A great deal remains to be discovered before model making of retinal units becomes a fruitful topic.

The Duplex Retina. The earliest correlation of retinal structure and function was undoubtedly achieved with Max Schultze's announcement of the duplicity theory in which rods were attributed with the role of receptors for scotopic vision while the cones were assumed to play that role in photopic and colour vision. At present there is no known means of correlating cone structure and the functional property of colour vision but the retinal densitometry measurements of Rushton (1958) and Marks's demonstration by microspectrophotometry have substantiated Young's theory of colour vision (1802) in its simplest form. In goldfish, monkey and man the cones were found to contain three pigments, with maximum absorption in either red, green or blue, segregated into separate receptors. This work eliminates the need for postulating a selective wave guide function for the outer segment (Bernhard, 1967; Waldron, 1967); a theory which probably grew up as a result of the continued failure to extract cone pigments from the vertebrate retina.

Cajal (1892) described second order cells which appeared to be linked either to the rod or to the cone receptors. The bipolar population was split into large, rod, bipolars and a smaller variety which connected only to cones. The horizontal cells were similarly subdivided into the external horizontal cells which lie scleral in the outer plexiform layer and connect with the cone pedicles and the inner variety which were described as connecting only to the rods. These observations were made on the teleost fishes but Polyak obtained similar results in the primate retina (1957) except in that the large rod bipolar was found to receive inputs from rods and cones. This finding has been confirmed by Stell (1966) who otherwise supports the findings of Cajal. The rod, or mop, bipolars were found to descend /

descent into the plexiform layer and give rise to a restricted terminal adjacent to the ganglion cell perikarya. The cone bipolars give rise to a more diffuse set of terminations which may spread out in any part of the inner plexiform layer but which only form synapses with the ganglion cell dendritic tree and not with the perikarya. Both types of bipolar connect with the amacrine cells but nobody has yet distinguished between amacrine connecting, say, to rod bipolars alone and another variety connecting with the cone bipolars.

The segregation of the retinal pathways into a predominantly rod channel and a separate pure cone channel has been confirmed physiologically. Gouras (1966) has shown that the b wave of the electroretinogram, which appears to arise in the bipolar cells (Brown, Watanabe & Murakami, 1965), contains rod and cone components between which no interaction can be demonstrated. An examination of the discharge in dark adapted monkey ganglion cells revealed, however, that convergence of the rod and cone components occurred at this level. Excitation of either rods or cones appeared to induce a refractory state to the passage of the other signal. If we assume the large bipolars to be carrying a mainly rod input to the ganglion cell perikarya, then the physical separation of these connections from the cone bipolar inputs on to the ganglion cell dendritic tree suggests the possibility of mutual inhibition arising between the two paths. This apparent physical segregation of the rod and cone inputs is, however, difficult to reconcile with the observation of Barlow et al. (1967) that both centre and surround receive uniformly distributed mixture of rod and cone projections. It will be noted that rod and cone interaction was not mentioned in the list of phenomena to be accounted for by a model of the centre surround unit. It must, of course, be added if the model is to be satisfactory.

Retinal Functional Lamination. The morphology and what is known of the physiology of the retina clearly reveals a lamination of function throughout its depth. Certain considerations suggest, however, that the organ may possess a greater degree of functional lamination than is at present indicated /

indicated by morphological examination.

It has been indicated that the ganglion cells of the concentric unit must connect with cells carrying the input for centre and surround and that the connection for each of these must be entirely of the on or off variety. In animals with colour vision, such as the ground squirrel or monkey, then the ganglion cells giving rise to concentric units must form, for the centre alone, only one of the following connections; red on, red off, green on, green off, blue on or blue off. The surround is generated by connection to the opponent colour population which is responding in the opposite phase to the centre and to no other cells. The connections under such circumstances may be achieved in the growing retina by some form of molecular specification but the system would clearly be facilitated if the various bipolars and amacrine types were organised so as to terminate in specific layers of the retina.

Such lamination is clearly revealed in the arrangement of the mainly red and pure cone horizontal cells and in the depth of ramification of the corresponding bipolar cells in the inner plexiform layer. Even the rod and cone receptor pedicles are spatially separated. Sjöstrand (1965) has found that bipolars with the most vitread nuclei terminate in the most sclerad position of the inner plexiform layer while those with nuclei adjacent to the outer plexiform layer terminate most vitread in the inner plexiform layer. This arrangement may reflect the difference between the rod and cone bipolars or indicate a more subtle lamination of function. In a recent paper, Ehinger (1966) has shown by fluorescence microscopy that the retinae of the rabbit and rat possess a variety of amacrine cells which ramify to give terminations bearing adrenergic synapses in the inner plexiform layer. In the rabbit there are three, and in the rat two, distinct laminae of adrenergic synapses which are distributed at the same level throughout the retina. Such methods may be the means for revealing the morphology of functional lamination but a satisfactory understanding of the relationship of the depth of dendritic tree ramification in the inner plexiform layer to the /

the functional characteristics of the units will probably only be achieved when the anatomy of specific cells which have undergone physiological analysis is studied. The technique for such work is already available (Thomas & Wilson, 1966).

Dowling's Theory of the Seat of Visual Adaptation. One of the more striking features of the vertebrate visual system is its ability to carry out visual discrimination over a range of illumination from threshold to some 10^{11} times more intense. The pupil can protect the eye from only a 10 fold increase in intensity. The process of visual adaptation has been shown to possess two components. Dark adaptation after exposure to bright light is limited by the rate of regeneration of the visual pigment (Hecht, 1937; Dowling, 1963). In light adaptation the incremental threshold is found to be linearly proportional to the log. of the background illumination intensity (Dowling, 1967) and adjusts to it in man within a period of less than 0.1 seconds (Crawford, 1947). The change of sensitivity in dark adaptation is equally rapid and unrelated to the pigment concentration unless the retina has been illuminated at levels some 10^7 time threshold when bleaching becomes significant. The rapid component of light and dark adaptation is understood as involving neural activity which may spread laterally within the retina. Rushton (1965) demonstrated that a background flash of an intensity such that only 10% of the rods could have received one quantum was sufficient to lower the sensitivity of the whole visual field to one third of its previous value.

Dowling (1967) has put forward a hypothesis as to the site of neural visual adaptation which is rather typical of the ad hoc models current in neurophysiological literature. The argument runs as follows:

1. Lipetz (1961) has demonstrated that when one region of a receptive field of a ganglion cell is light adapted then the sensitivity is diminished in other regions. The finding has been confirmed in essence by Easter (1968).

Dowling interprets this result as indicating that neural visual adaptation occurs centrally in the retina where lateral inhibition can take place but /

but with Sjöstrand's (1958) demonstration of lateral processes between receptors and the known lateral interconnection of the receptors through the horizontal cells this means little more than that the outer segments are not involved in this stage of visual adaptation.

2. The b wave of the ERG has adaptation properties similar to those of the psychophysical adaptation (Johnson & Riggs, 1951) and to the ganglion cell but is present in retinæ in which the ganglion cells have degenerated. Other evidence (Brown, Watanabe & Murakami, 1965) indicates that this wave arises in the bipolar layer.

3. The a wave - which is usually attributed to the receptor activity (Brown et al., 1965) - does not, according to Dowling (1967), show an incremental sensitivity curve similar to that of the b wave because it saturates at a value of background illumination intensity well below that of the b wave.

Dowling concludes that the a wave can play no direct part in the generation of the b wave and it is suggested that it does not arise in the receptors but in the same site as the S units, whose incremental sensitivity curve it matches. The very convincing evidence of Barlow et al. (1965) to the effect that the a wave originates in the receptor is discarded without further consideration.

Dowling concludes this part of the argument:

"... the b wave is the first response of the visual system to show typical adaptation to background light - that is, adaptation similar to psychophysical adaptation. Thus it seems likely that the main site of adaptation in the visual system is located in the bipolar cell layer."

The site for adaptation is suggested to be the reciprocal junction between bipolar cells and the amacrine cell (Dowling & Boycott, 1966). The local feedback from the stimulated amacrine is assumed to reduce the sensitivity or gain of the bipolar cell in proportion to the extent of its excitation. The lateral spread of adaptation could occur through the amacrine cells to other bipolars /

bipolars and account for Lipetz's results.

The statement underlined above does not necessarily follow from the evidence. The difference between the a and the b waves described by Dowling does not conclusively exclude the a wave from involvement in the production of the b wave but if this is the case, and the a wave is not in the direct path of b wave production, then some other, unknown, process must transfer activity along the receptor-bipolar path. There is no evidence to indicate that this process does not show adaptation similar to the b wave and an argument based upon the conclusion that the "b wave is the first response of the visual system to show typical adaptation ..." is somewhat unsatisfactory.

The work of Gouras (1966) has indicated the independence of rod and cone components of the ERG b wave. The results of Stiles (1959), Alpern and Rushton (1965) and du Croz and Rushton (1963) have shown that visual adaptation of rods and each of the various cone channels occurs independently. Change, for example, in the red background illumination has little effect on the sensitivity of the green mechanism. This separation of the channels indicates that the "adaptation pools" or cells involved in the lateral spread of neural adaptation (Lipetz, 1961; Easter, 1968) must be segregated - each receiving the input of only one receptor type. Now both centre and surround of the receptive field of a retinal ganglion cell have rod and cone input (Barlow, Fitzhugh & Kuffler, 1951) with apparently similar spatial distribution as indicated by the area/threshold curves. If, as Dowling and Boycott (1966) have suggested, the surround of the receptive field is generated by amacrine cells then these cells would have to receive both rod and cone input. Such an amacrine cell could not, however, be the site of the adaptation pool because the lateral spread of adaptation information would carry a mixture of rod and cone messages to the connected bipolars with the consequence that the increment sensitivity of the two systems would not be independent.

It would be possible to retain Dowling's suggestion of amacrine/bipolar feedback as the basis for visual adaptation if Dowling and Boycott's concept of /

of the surround were extended by postulating that the surround region of a receptive field is generated by the summation of independent rod and cone surrounds - formed in separate amacrine - at the ganglion cell levels. If this is not the case then it must be concluded that the b wave adaptation reflects a process occurring before the amacrine feedback and most probably before the bipolar cell itself.

The suggestion of separate rod and cone amacrine has been introduced only to show how Dowling's hypothesis may be preserved but no direct evidence supports such an arrangement. In addition, as we have seen, the assumption upon which Dowling's idea is based neglects the role in light adaptation of processes occurring at the receptor bipolar level. Therefore, it is worthwhile considering this region as the seat of visual adaptation.

There is general agreement that the b wave originates in the bipolar cell (e.g. Brown, Watanabe & Murakami, 1965). If Dowling's hypothesis is accepted, then we must assume either that the b wave originates in the terminal region of the bipolar or that the b wave reflects the activity of the bipolar perikaryon and dendrites but that this is subject to the influence of the distant amacrine feedback. Since Brown and Wiesel (1961) have shown that the region of maximum amplitude of the b wave is located at the junction of the outer plexiform and inner nuclear layers it appears more probable that the first suggestion is not the case and that the b wave represents activity of main part of the bipolar cell. It is unlikely that the localised amacrine feedback could influence activity in this region to a great extent and I suggest that the b wave shows adaptation because this process is carried out before the bipolar cell.

Both Polyak (1957) and Stell (1966) have described the bipolar population of primate and teleost retina as consisting of rod or mop bipolars which connect to both rods and to cones and cone bipolars which connect to cones alone. The previously mentioned adaptation independence of rod and cone channels suggests that light adaptation occurs before the rod and cone inputs are mixed in the mop bipolar and must thus be considered to occur /

occur before the bipolar cell.

Teleological considerations would also suggest that light adaptation should be carried out at an early stage in the processing of visual information within the retina - preferably, for simplicity, before the receptor output is converted into a variety of 'on' or 'off', rod and cone channels. If bipolars form 'on' and 'off' classes, it is difficult to imagine how visual adaptation could be arranged for the 'off' group with equal facility to the 'on' by means of amacrine feedback.

The results of Cajal (1893), Stell (1966) and Yamada and Ishikawa (1965) indicate that a given horizontal cell in teleost or mammal shows connections either to rods or to cones alone. The horizontal cells would thus appear to possess at least one of the necessary qualities required by an adaptation pool - although it remains to be seen whether, say, only red cones connect to one horizontal cell. Little is known about the functions of the horizontal cell but they are clearly in a position to effect control over transmission from receptor to bipolar; their lateral spread is adequate to account for neural adaptation and they are situated, as the above argument requires, distal to the bipolar cells.

Unpublished work in this laboratory has indicated that, in the rabbit, the ratio of receptor nuclei/inner nuclear layer nuclei remains fairly constant from top to bottom of the retina at a value of about 11:1 which is independent of receptor density variation between area centralis and periphery. A similar tendency for constancy of the ratio has been noted in the results of Chievitz (1891) in the cat. The inner nuclear layer/ganglion cell nuclear count ratio varies considerably over the same region. The results suggest a uniformity of function throughout the retina in the outer plexiform layer. Such uniformity would be expected if this layer were organised to carry out the neural component of visual adaptation because provision for the process would not be a function of the ganglion cell density in the region.

The above suggestions are supported by recent work which was not available /

available to Dowling. Naka and Rushton have described the S potential as originating in a thin layer of retina at about the horizontal cell level (1967). In a later paper (1968) they show that the process of visual adaptation must have occurred in a region functionally preceeding the generators of the S potential. It is sufficient to note that this means that light adaptation occurs distal to the junction of the inner nuclear and outer plexiform layers.

SUPERIOR COLLICULUS

Evidence as to the role of the colliculus is available from two main forms of behavioural experiment.

EVIDENCE FROM COLLICULAR LESIONS

In birds and frogs the majority of the optic nerve fibres pass to the tectum which is the midbrain visual centre homologous to the superior colliculus in mammals. Destruction of the tectum in these animals appears to result in complete blindness (Bechterew, 1884) while removal of the fore-brain which leaves the tectum intact does not interfere with many aspects of visual behaviour, in Visser and Rademaker, (1935a & b).

Early work indicated a similar importance of the superior colliculus in the visual system of the mammals. Thus Flourens (1842) found total blindness in rabbit, rat and dog after collicular lesions. These results were confirmed by Bechterew (1884) who pointed out that the visual deficit was only accompanied by motor disturbances if the lesions involved the underlying tegmentum.

Layman (1936) found that rats were able to be trained to accomplish pattern and intensity discrimination after large subtotal collicular lesions. Similar results were obtained by Lashley (1937). More recent work on the cat by Sprague and Meikle (1965) appears to confirm this finding rather than that of the older literature. Unilateral lesions to the superior colliculus which did not involve the tegmentum resulted in

1. homonymous field defect with neglect of stimuli in the visual fields contralateral to the lesion.

2. motor deficit in the appropriate eye, head and body movements, which was expressed in ipsiversive forced turning.

It was noted that the motor deficit could be obtained alone by lesions to the tectospinal path while visual neglect without forced movement could be obtained after section of the brachium of the superior colliculus. Bilateral collicular lesions followed by an apparent initial blindness, which disappeared in a few days, and permanent deficits in visual following and localisation /

localisation of stationary stimuli. Although pattern recognition was not tested, the visual recognition shown by the animals was apparently normal. Myers (1964) found that complex pattern recognition was not influenced by collicular lesions in the cat unless the tegmentum became involved.

The results in the literature dealing with the monkey are difficult to interpret. Bender, Pasik and Pasik (1957) describe little deficit in eye-movements after the bilateral ablation of the colliculus. Rosvold, Mishkin and Szwarcbart (1958), however, describe restricted eye movements accompanied by normal visual discrimination. The results obtained by Denny-Brown after collicular ablation in the macaque (1962) are very similar to those obtained from the cat by Sprague and Meikle. Hemianopia and circling are described while bilateral ablation resulted in lasting fixation inaccuracy and continued lack of visual responsiveness.

The above work and other material has been very competently reviewed by Schneider (1966) who suggests that the variety of results obtained from primates by recent workers may be explicable on an anatomical basis. The superior colliculus receives a considerable input to its deeper layers from the visual cortex. Shallow lesions might leave these paths fairly intact and give results similar to those of Pasik and Pasik (1964) while deeper damage could give rise to results like those of Denny-Brown (1962).

In an attempt to clearly define the effect of collicular damage, Schneider undertook to examine the visual behaviour of golden hamsters which had been subjected to total undercutting of the superior colliculus. After the operation the animals initially behaved as if blind when tested upon the visual localisation of foodstuffs and would not give orientating responses of head and eyes to visual or sound stimuli. On the other hand, it was noted that they gave a greater percentage of 'freeze' responses to stimuli than did normal animals so that they were at least able to detect the stimuli. Total destruction of the superior colliculus left the ability to learn pattern discrimination unchanged and the animals showed normal exploration but considerably reduced head movement during their examination of /

of the visual environment. The restricted head movements were not, however, the result of motor deficit of a general nature because such movements were present during grooming and digging. This work thus suggests that the superior colliculus is involved in orientation to stimuli but not necessarily in the direction of attention as the freezing and avoidance reactions remain.

There is sufficient evidence to suggest that the colliculus plays an important role even in the primate and should not be regarded as a vestige of the submammalian visual system. The interpretation of ablation studies is, however, always fraught with difficulty because it is impossible to confine the damage to one region or know whether the phenomena observed result from injury to fibres present merely en passage. We thus refer to the results of a set of complementary studies.

ABLATION OF THE STRIATE CORTEX

The majority of the optic tract fibres project either to the LGN, and thence almost entirely to the visual cortex, or to the superior colliculus. It has long been assumed that removal of the cortical visual areas reveals a residue of visual behaviour which is mediated predominantly by the superior colliculus. The extent of the residual subcortical visual behaviour is indicated in the earlier literature to vary from apparently complete blindness in the monkey and man to the retention of a considerable degree of visually guided behaviour in the lower forms. Early work on the rabbit by Ten Caate and Van Herk (1933) and Ten Caate (1935) revealed that a de-striate rabbit could respond to visual stimuli, movement and lights, run between obstacles and both search for and recognise food by visual cues. The animal retained OKN in response to movement of its whole visual field. The presence of OKN response has been demonstrated in decorticate cat, Scala and Spiegel (1941), dog and monkey (Rademaker and Ter Braak, 1948).

Lashley (1931; 1939) demonstrated that rats became incapable of being trained to distinguish between patterns after the removal of striate cortex on both sides but that they could discriminate between sources of light at different total intensities and could discriminate objects well enough /

enough to jump between stands. Similar results with respect to intensity judgements but not to object vision were obtained from the monkey by Klüver (1942) who suggested that monkeys without the visual cortex lost the sense of "... visual space with all its dimensions".

The results from the rat appear to be similar to the findings of Ten Caate et al. on the rabbit but they conflict with those from the monkey. It is only more recently that the necessary detailed examination of residual visual behaviour in de-striate animals has become available in such a form to help resolve the problem.

Schneider (1966) made an examination of the visual behaviour of de-striate golden hamsters. In spite of large lesions to the visual cortex on both sides, the animals could localise food objects by visual means and orientate to sounds. Two in five were unable to distinguish black from white, four in five failed to distinguish horizontal from vertical stripes and all five failed to distinguish a speckle pattern from diagonal lines though all could discriminate between the speckle and a grey of equal reflectance. The cortical visual field was concluded to be involved in the process of pattern recognition but not in that of orientation to stimuli. It must be noted, however, that the cortical striate ablations were not total. The ablation of the striate cortex in the tree shrew has recently been described as having no obvious effect upon the visually guided behaviour (Snyder, Hall & Diamond, 1966). Such results substantiate the findings of Ten Caate in the rabbit.

A remarkable finding by Sprague (1966) has emphasised the need for caution when negative results are obtained. After a very extensive right occipital lobe lesion, the cat was found to evince complete hemianopia of the left visual field and would follow stimuli only to the right. Immediately after lesions had been placed in the left superior colliculus it was found that the left visual field recovered their sensitivity to stimuli which was lost permanently if the right colliculus was destroyed. Thus the colliculus on the side of the cortical lesion was prevented from revealing its /

its potentiality for responding to moving stimuli (not to stationary objects) by inhibition which was demonstrated to pass through the commissure of the superior colliculus. Fischman and Meikle (1965) have also recorded the ability of the decorticate cat to localise moving objects.

Recent investigations have revealed that the monkey also does not differ as much as was thought from the lower animals. Pasik, Pasik and Krieger (1959) report that de-striate monkeys will track large visual stimuli and reach out to a light while Weiskrantz has shown that some discrimination is possible when stimuli are matched for luminous flux (1963). The most striking findings have been reported by Humphrey and Weiskrantz (1967) after work on long term de-striate animals (5 and 19 months post operative). The animals were found to be capable of reaching out for a moving object, such as the experimenter's hand, and certainly retained sense of visual space. Training revealed that objects as small as a 0.25" cube could be detected and reached for if moved only slightly. The tremor of the hand holding the stimulus was adequate to ensure detection. Flashing neon lights are readily detected and the animals subsequently became able to detect even small stationary objects against an illuminated background. In view of this last remarkable finding it is most unfortunate that the necessary histology has not yet been carried out because the animals have been kept alive for further work. It is possible to account for the results if a small remnant of the visual cortex remains intact. The authors counter this criticism by pointing out that only the peripheral field could be represented in the remaining cortical tissue and that the sensitivity of the de-striate monkeys is greatest for stimuli in the central region of the visual field. Although the effect of lesions to the colliculus in these animals has not been determined there is little doubt that the visual information available to the animal is processed through this organ. The spatial localisation evinced by the monkeys, which cannot, however, judge distance, is remarkably similar to that of the golden hamster as demonstrated by Schneider (1966).

SUBCORTICAL VISION

The usual problems of ablation experiments must be borne in mind during the consideration of the above results but questions other than whether the lesions were confined to the regions specified arise. In view of the recently established multiple projection from the LGN to the visual areas 17, 18 and 19 in the cat (Wilson & Cragg, 1967), it is apparent that removal of area 17 alone, in this animal, cannot be regarded as a suitable lesion for revealing the subcortical visual powers. A similar situation may exist in the rabbit. Squire (1967) has, in fact, commented that it is necessary to remove areas 17, 18, 19, middle and auditory cortex if hemianopia is to be complete in the cat. The removal of area 17 alone in the monkey (Humphrey & Weiskrantz, 1967) is probably adequate because areas 18 and 19 do not appear to receive projections from the LGN (Covey, 1965). Lesions must be established as total for behavioural work following ablation to be entirely acceptable. Very complete compensation in visual behaviour has been reported after lesions claimed to involve 99% of the optic tract in cats (Galambos, Norton & Fromer, 1967) or 59/60 of the visual cortex in rats (Lashley, 1935). It is encouraging, therefore, to find that the failure of orientation to visual cues after collicular lesions is complemented by the failure of almost all spatial vision other than orientation to visual stimuli in the case of cortical lesions.

The various species thus appear to be much more similar in their subcortical visual apparatus than might be thought from the early literature. It should not be imagined, however, that collicular role in subcortical vision is to be regarded as identical in rabbit, cat and monkey. The rapid, spontaneous, acquisition of visually guided behaviour by the decorticate rabbit is very different to the case of the monkey which requires training to develop the use of its latent extra-striate localisation mechanism. It is of interest to note that a number of cases of human subjects with striate lesions have been reported in which movement perception is retained in the blind region (Riddoch, 1917; Holmes, 1919). It is thus possible that extra /

extra-striate vision is present in man.

Recent work on subcortical vision thus does not support the concept of progressive encephalisation of visual function as it was put forward by Marquis (1935):

"Within the mammalian series, from the rodents to the primates and man, there is a progressive shifting of visual functions from the superior colliculus to the striate cortex."

and may often be found in the recent literature. The concept is sometimes supported by comparison of the number of retinal fibres projecting to the tectum in different animals. Brouwer and Zeeman (1926) may be quoted to the effect that few optic tract fibres reach the tectum in the monkey while an inverse arrangement may be implied in the 'lower' animals:

"In the rabbit, most of the afferent optic fibres from the right eye project chiefly on to the left superior colliculus (somewhat also on to the geniculate body)."

Monnier (1967).

In fact, no comparative counts of the number of optic tract fibres passing to the LGN, pretectum and superior colliculus have been made. The projection to the LGN in both cat and rabbit is considerable. It may be that the proportion of fibres projecting from the visual cortex to the superior colliculus increases in passing from the rat to monkey but this does not imply that the retinal projection plays any lesser role or even decreases in absolute terms. A more detailed critique of the theory of encephalisation has been put forward by Pasik and Pasik (1964).

It was mentioned earlier that the removal of the striate cortex is usually assumed to reveal predominantly collicular function. An examination of the literature reveals, however, a dearth of control experiments in which collicular lesions are made subsequent to recovery from occipital lobectomy or decortication in order to demonstrate that this organ is an important factor in the residual visual capacity. In such cases in which the experiments have been carried out they are usually acute and leave little time for the recovery of residual powers. The subcortical visual capacity may thus be /

be mediated by at least the accessory optic tract, LGN, pretectum or colliculus. Of these, the LGN is usually excluded on the basis that it projects only to the cortex but Marchiava and Pepeu (1966) have claimed to physiologically demonstrate a projection from the LGN to the superior colliculus in the cat. Such a connection has been referred to in the anatomical literature by a number of workers (Altman, 1962; Cragg, 1962; Gudden, 1886), while Altman (1962) has mentioned projections to pretectal and thalamic nuclei in the cat. The accessory optic tract is similar to the LGN in that it remains an unknown factor and consequently tends to be neglected. The pretectal area and superior colliculus have, however, been shown to be involved in mediating subcortical visual behaviour which may be considered as containing the following elements:

1. Blink reflex
2. Pupillary reflex
3. Light-dark discrimination
4. Optokinetic nystagmus
5. Movement location, stimulus tracking and simple pattern discrimination.

The blink reflex has been securely established as not requiring the superior colliculus for its generation (Levinsohn, 1904) in the rabbit while Pasik and Pasik (1964) have demonstrated its presence in monkeys which lack the superior colliculus and striate areas. In a similar fashion, Magoun (1935) has shown that the pupillary reflexes remain unimpaired after lesions to the superior colliculus but that bilateral destruction of the pretectum (Magoun & Ranson, 1935) abolishes all pupillary reflex movement. More recently Urbaitis and Meikle (1968) have demonstrated that cats are able to learn simple light-dark discrimination tasks after removal of the posterior neocortex and superior colliculi. It is natural, therefore, to wonder about the extent to which the evidence supports the attribution of the other visual powers remaining in de-striate animals to the superior colliculus.

Subcortical, field holding, optokinetic nystagmus has generally been assumed to arise in the superior colliculus. This assumption is so engrained /

engrained that it came as a considerable surprise to the author when it was discovered, upon investigating the literature in detail, that the evidence for the view is rather poor. Rademaker and Ter Braak (1948) have investigated the phenomenon in detail in rabbit, cat and monkey but do not describe control lesions to the colliculi of decorticate animals which display OKN responses. In the case of the cat, Scala and Spiegel (1938) are usually referred to but the impairment of OKN subsequent to collicular lesions was examined for only a short period after the operation. The most frequently quoted observations are those of Smith and Bridgeman (1943) on OKN in the guinea pig. Examination of the paper reveals, however, that the observations were carried out on head nystagmus and that eye movements were not recorded. Conclusions about the latter may thus not be drawn. Smith and Bridgeman (1943) refer to Smith (1941) upon the point of correspondence between eye and head nystagmus but the matter is not treated in the latter paper. In no case were both colliculi and striate areas removed to demonstrate the disappearance of head nystagmus. A less frequently quoted paper, Smith (1939), contains a very brief account of the necessary control experiments in which bilateral lesions to colliculi and striate cortex are described as producing deficiencies in OKN but not as eliminating the movements. The results are stated to be similar whether the cortex is removed with the colliculi or not. Diagrams in the Smith and Bridgeman paper indicate that in this latter case there is still extensive head nystagmus. The suggestion that OKN can occur in the absence of visual cortex and colliculus is strengthened by the reports of Pasik and Pasik (1964) and Bender (1962) to the effect that bilateral occipital lobectomy followed by bilateral destruction of the superior colliculus fails to abolish OKN in the monkey. Urbaitis and Meikle (1968) have commented that they were able to elicit OKN in cat after combined lesions to the colliculi and posterior neocortex but the extent of the lesions in these cases is not quoted.

The best behavioural support for the role of the superior colliculus - rather than other subcortical centres - in visual tracking is probably the previously /

previously mentioned complementary ~~effects~~ effects of striate and collicular ablation. The conclusive evidence that tracking of moving objects by the de-striate guinea pig or monkey fails upon collicular ablation is not available. Sprague (1967) has shown, however, that such tracking fails in the case of a cat subjected to striate cortex and collicular ablation. The difficulty of eliciting even a light/dark discrimination from a de-striate and colliculectomised cat (Urbaitis and Meikle, 1968) suggests that more sophisticated discrimination, such as horizontal from vertical stripes as described by Schneider (1966), would fail upon destruction of the colliculus in a de-striate guinea pig or cat.

OCULOMOTOR ROLE OF THE SUPERIOR COLLICULUS

The superior colliculi were first claimed to be motor centres for eye movements by Adamuk (1870) upon the basis of electrical stimulation experiments. Holmes (1938) and Crosby and Henderson (1948) have developed this idea and describe the superior colliculi as centres through which the cortical visuomotor areas operate the eye muscles.

Extensive destruction of the superior colliculus in rabbit (Topolanski, 1898) and cat (Spiegel & Scala, 1937) does not, however, impair eye movements elicited by stimulation of the occipital lobes or of the frontal region in the cat. The findings of Pasik and Pasik (1964) in the cat and monkey confirm these results. The colliculi thus do not provide the only cortical oculomotor outflow. A straightforward motor relay function for the superior colliculi appears even more unlikely when it is considered that no direct fibres from these organs to the oculomotor nuclei have been traced in cat or rabbit while those claimed to be present in the monkey by Crosby and Henderson (1948) have not been confirmed. The absence of such fibres is also suggested by Hyde and Eliasson's (1957) observation that the latency of eye movements obtained upon stimulation of certain regions of the pretectal nuclei or tegmentum are of shorter latency than those elicited from the superior colliculus. Szentagothai (1950) presented evidence that the superior /

superior colliculi project to the pretectal nuclei which have been described as having projections to the oculomotor nuclei (Szentagothai, 1943). Altman and Carpenter (1961) have described the nucleus of Darschewitsch and the interstitial nucleus as receiving projections from the superior colliculus and thus confirm Szentagothai. Hess and Hassler (1954) have shown that electrical stimulation of these nuclei produces specific turning movements of the head and eyes in the cat. The output of the superior colliculus may thus be processed in complex fashion before it reaches the oculomotor nuclei. Such an arrangement may be necessary for the integration of eye and head movements. There is not the space to become involved in the complex and debateable literature on the physiology of horizontal and vertical eye movement control. Interspecies differences are likely to be considerable and no work appears to have been carried out on the rabbit whose organisation is likely to be very specialised. Schaefer (1960) has, however, described limited head and leg movements upon stimulation of the rabbit superior colliculus but histological data indicating the depth of stimulation was not given.

Topical stimulation of the superior colliculus by a small crystal of strychnine led to directed movements of the head and eye in the lightly anaesthetised cat (Apter, 1945). The final point of regard of the eyes was found to correspond with the coordinates of the visual field representation at the point stimulated on the superior colliculus. This correspondence of the sensory and motor maps provides an obvious basis for the tracking role indicated by the behavioural experiments. The coincidence of the topographical projections from retina, VI, VII and prestriate regions to the different levels of the colliculus provides the anatomical substrate for control of such a tracking system. It was consideration of the apparently directed eye and head movements obtained upon stimulation of the superior colliculus in the cat that led Hess, Burgi and Bucher (1946) to describe the colliculus as a centre for the "visual grasp reflexes" involved in tracking moving objects. Their suggestions have in essence been confirmed by later work.

Pasik /

The multiplicity of projections to the superior colliculus and its apparent remoteness from direct control over the eye muscles suggest that it functions as more than a motor relay nucleus. The fact that the colliculi appear to be necessary, in the absence of the striate cortex, for the retention of certain less complex visual functions tends to confirm this view. It must be confessed, however, that there are a number of possible ascending paths from the colliculus which may be intact in the de-striate animals. The colliculus has been described as projecting to the midline thalamic nuclei and to the pulvinar in the cat and hamster and some projections may reach the cortex - perhaps via the reticular formation. The whole pretectal region also remains intact in these animals. The work so far described has indicated a great deal but the very nature of ablation experiments obviates any clear decision as to the collicular role. It is not possible to discriminate between the effect of a lesion which eliminates one stage from a path over which a function is distributed from one which eliminates the stage at which the function is located. Single unit studies offer information about the data processing going on at one particular stage. Such single unit work as has been carried out tends to confirm the collicular role indicated in the above sections.

SINGLE UNIT FUNCTION IN THE RABBIT SUPERIOR COLLICULUS

The investigations of the rabbit collicular single units which are reported here support Schaefer's (1965) finding of a markedly laminar arrangement of the various unit types in this species. A detailed examination of the unit distribution in depth has not yet been reported for other mammals. Consideration of the properties of rabbit collicular units in conjunction with the anatomy of the organ enables a qualitative and admittedly speculative account of how the superior colliculus functions to be given. Comparison with other mammals will be made subsequently.

The incoming retinal fibres have already been described as entering the superior colliculus from the brachium, passing horizontally in the stratum opticum and then turning upwards into the stratum griseum superficiale. It has also been demonstrated that the single units of the upper stratum griseum superficiale (SGS) are remarkably similar in properties to the multiunit evoked response of that region. They both -

1. Show evidence of an inhibitory surround;
2. Evince prolonged firing at off of a centred light spot but a relatively brief on response;
3. A good response to shadows or to very small movements of an object within the receptive field;
4. Ability to respond to fast movement;
5. Give a dimming but not a brightening response to step changes in light intensity.

In fig. we show off, on, dimming and rapid movement responses for an optic nerve large field off unit, a single unit from the upper SGS and for the multiunit evoked response of the upper SGS. The similarity of the three responses is very evident.

Single units of the large field off type may be found in optic nerve, brachium and stratum opticum as well as in the upper part of the SGS. It is suggested that these units project in quantity to the upper SGS and thus give rise to the major component of the multiunit response and predominate in determining its properties. The single units of this region which possess the same properties as the large field off type of the optic nerve have in some cases definitely been identified as cells by prepotentials or injury /

injury discharge. The multiunit response may, however, represent the massed activity of terminal arborisations of retinal axons rather than of the collicular cells.

Levick (1965) has described the large field ~~of~~ unit of the optic nerve as an 'alarm unit'. It would appear that these units project to a very appropriate region of the brain if the subjective impression of the unit response indicated by his nomenclature is significant. We may envisage the upper part of the SGS as receiving the projection of this class of units from all parts of the retina in topographic fashion so that the terminals form a map of the visual field. There is normally very little spontaneous activity in this region of the superior colliculus so that a burst of firing within the layer will indicate the presence of 'activity', e.g. movement or a shadow, at an appropriate point on the map. The layer may be imagined as an early warning display fed by a population of 'alarm' units.

It may be remembered that it was shown in an earlier section that the superior colliculus map contains a more extensive representation of the upper visual field than does the geniculo-cortical pathway in the rabbit. A similar difference of representation of the upper field is to be found in the cat (Vejbaesya, 1967). This topographical feature may readily be integrated into the concept of the colliculus acting as an 'observer' for novel activity. It may also be significant that the upper part of the SGS ^{of the rat} is found to be free from cortico-tectal projections - except perhaps for a small descending component from the stratum zonale. In the absence of such connections it would appear that the region is autonomous of cortical control and provides an independent display of retinal events. It may play a part in activating the subadjacent regions of the colliculus, where cortical projections are well represented, and thus institute an orientating reaction, which is subject to cortical modulation, to the region of visual space represented in the column.

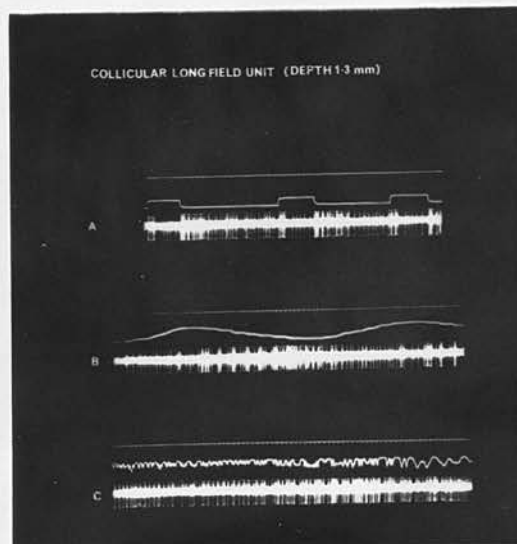
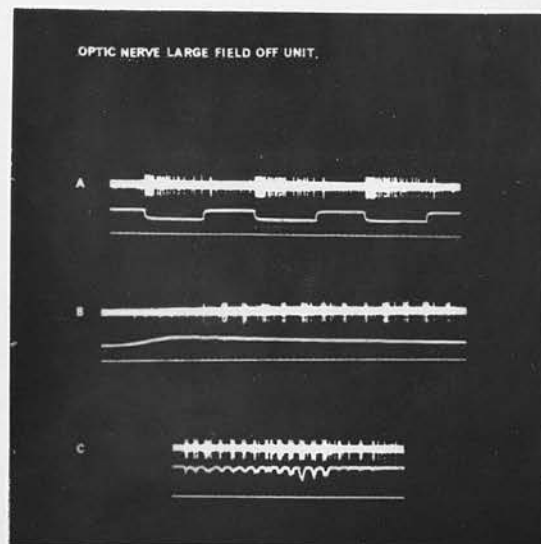
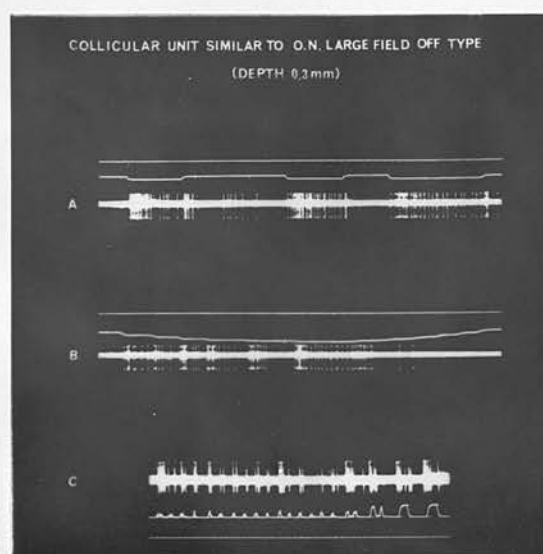
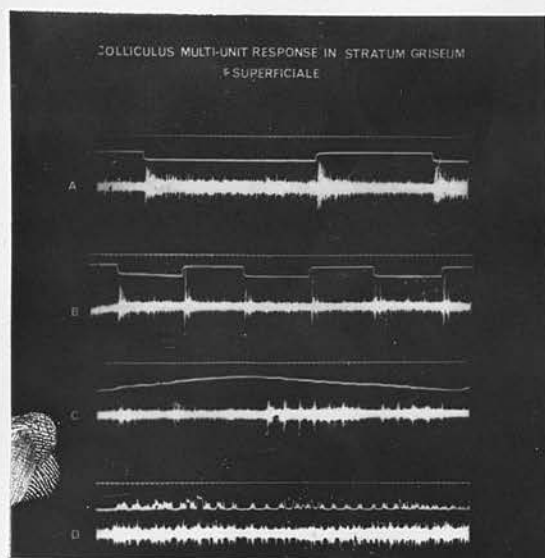
The optimal stimuli for the units of the upper part of the SGS are remarkably similar to those required to elicit visually directed behaviour in /

in animals lacking the cortical visual areas. The responses of the rat (Humphrey, 1968) and rabbit upper colliculus remain unchanged after cortical ablation. It would thus appear that the necessary information for directed movements in such animals passes directly from the retina to the superior colliculus. The simplest interpretation of the ablation studies - that the colliculus alone mediates the more sophisticated subcortical directed visual behaviour - appears to be justified by the unit studies on the upper part of the colliculus alone. A preliminary report of the experimental findings described above has been published (Hughes, 1968).

Amongst the units of the stratum opticum and the stratum griseum intermediale are the long field units which possess a 100° diameter weak on or off-on field divided by a predominantly off band of up to 100° long by 20° wide. The band is sensitive to flash but is the only region of the field which responds to moving card stimuli. The movement, dimming and off flash responses of the band region are similar to those of the alarm units isolated from the SGS and examples of the responses of a long field unit are included in fig. 10g for comparison with those of the large field off unit. The vertical organisation of the colliculus (Cajal, 1911) is consistent with the suggestion that the axons of the SGS alarm unit cells project to the underlying cells of the stratum opticum and intermediale and there converge to generate the band shaped fields. The long field units with their potentially greater vertical than horizontal resolution, may be involved in the maintenance of images on the long narrow area centralis of the conscious rabbit.

The single unit properties which appear in the deeper layers of the rabbit superior colliculus are consistent with what would be expected if the organ were to carry out the functions indicated by behavioural work on animals subjected to cortical occipital lobectomy. Few of the units encountered below the stratum opticum would respond well to flashing of a light spot although movement was a very adequate stimulus. Directional units were encountered in the stratum opticum but these were of the retinal type and appeared /

Fig. 108 Selected responses of massed collicular units, optic nerve large field off units, collicular large field off unit and a collicular long field unit. See page 236.



appeared to be fibres. In deeper regions, directional responses were found but were not as clear as those in the retina. There was rarely a null direction and sometimes responses disappeared while under examination. Schaefer has noted that the directional units at the vertical meridian show centrifugal preferred directions and those in the peripheral field a centripetal preferred direction which might suggest the role of maintaining an image at the centre of the streak for the central units and for bringing an image to that region for the peripheral units. The refractory nature of the deeper collicular units has been noted by a number of observers (e.g. Horn & Hill, 1966) and an example of habituation, which is relatively stimulus specific, has been given earlier. It seems unlikely that the phenomenon is the result of anaesthetic interference as it is repeatable under various conditions. It is possible that these cells are involved in the elimination of responses to non-novel stimuli but, in view of the short duration of the single unit habituating phenomenon, it would be unwise to suggest that it provides a mechanism for the habituation of the orientating response (Sokolov, 1963). In the deepest parts of the colliculus are to be found the very large quadrant or hemifield units with receptive field boundaries running exactly along the vertical and horizontal meridia. It is tempting to assume that these units represent a motor outflow from the colliculus but there is no direct evidence available to substantiate this.

We thus speculatively envisage that the collicular functional column in the rabbit consists of

1. alarm and activation
2. generalisation for maintenance on the streak
3. movement detection
4. direction analysis for field stabilisation and tracking
5. elimination of responses to re-occurring stimuli
6. quadrantly subdivided motor output to head and eye movement centres.

It must be remembered, however that this tentative scheme deals only with the role of the organ in the de-striate preparation and ignores the function of the extensive cortical projections in the normal animal.

TECTAL UNITS IN OTHER MAMMALS

The literature on the single units of the superior colliculus of animals other than the rabbit does not indicate a universal identity of properties but, in spite of differing investigative techniques, the properties are similar in several ways. It is clear that in rat, cat, rabbit and monkey as well as frog and pigeon, the receptive fields of superficial units are smaller than those of the deeper units.

The upper part of the rat colliculus (Humphrey, 1968) has a population of small field units with a predominance of off responses and later inhibition. The units are sensitive to movements but are bigger than the apparently similar alarm units of the rabbit ($2-15^\circ$). Small field units appear in the upper parts of the stratum griseum superficiale in the cat (Vejbaesya, 1968) which, like the units of rabbit and rat, show poor response to an extended edge ($2-3^\circ$ centre). The superficial small field units of the monkey colliculus (Humphrey, 1968) respond better to light than to dark stimuli and do not show pronounced lateral inhibition and no claim is made by Humphrey that these units resemble those of the upper part of the rat colliculus.

The deeper units of the rat colliculus also resemble those of the rabbit in that many of them have receptive fields markedly elongated along the horizontal axis (Humphrey, 1968). The eccentricity and size of these units is not as great as in the rabbit but, as in the latter animal, their properties are said to be similar to those of the more superficial small field units. There is at present no indication that the rat possesses any form of visual streak so that the suggested role for the rabbit long field units - that of maintaining an image on the retina at the level of the streak - appears less likely because both species possess such similar units. The presence of such elongated receptive fields has not been reported in investigations on the cat colliculus (Vejbaesya, 1967; Mollwain & Buser, 1968, etc.) but the results of Marchiafava and Pepeu (1966) would indicate the presence of large fields, sensitive to movement, and of distinctly oval form, /

form, although not orientated parallel to the horizontal as is the case in the rat and rabbit. It is interesting to note that the units responding to large angular movements of stimuli are said, by Marchiafava et al., to disappear upon damage to the LGN which leaves the direct retina-collicular path unharmed. They remain, however, after acute ablation of the neocortex. The long field units of the rabbit are very similar to certain units found at the rear of the LGN and interconnections between LGN and superior colliculus have recently been reported. It is thus possible that these units arise in, or adjacent to, the LGN and not within the superior colliculus. They do not arise at cortical level because they are found in the decortical animal. Markedly oval fields have not been reported in the monkey.

Directional units appear to be one of the major sources of difference between the accounts of the superior colliculi of the various species studied. Neither Humphrey (1968) nor Simonoff, Schwassmann and Kruger (1967) were able to find directional units in the rat tectum. In contrast Schaefer (1966) describes 70% of the units of rabbit tectum - especially those of the deeper layers - as directional. This contrasts with Hill's report (1966) of 20% of these units in the same animal. In the present work only 5% of the units were found to be superficial on-off directional units of the retinal type although many deeper units of the refractory kind evinced asymmetric response of a directional nature. The difference in the percentage of directional units reported by Schaefer and by Hill for the same animal may result from Schaefer having mistakenly grouped long field units in this class. His criteria for directionality are not clear and he worked with free moving animals. It is uncommon to find the contrast reversal test quoted to establish directionality of response for central units and some errors may arise during the study of asymmetric central units which will not respond to light spots and therefore cannot be accurately located. Barlow et al. (1963) have shown how easy it is to identify a unit as directional when it is not, if tests are carried out before the receptive field is mapped with a light spot. Directional units are reported in quantity in the /

the case of the cat but even here the figures vary considerably; thus directional units form 14% (Vejbaesya), 64% (McIlwain & Buser), 78% (Straschill & Taghavy) of the tectal population. Vejbaesya (1967) has described two populations of directional units in the cat. The upper regions contain units responding to movements of optimum velocity of about 30°/sec. in centrifugal and centripetal or other directions. Another population was found in the stratum griseum intermediale which responds only to very fast centripetal movements (100-300°/s.). This finding would resolve the conflict between McIlwain et al. (1968) and Straschill et al. (1967) over optimal velocity if the latter neglected the deeper units. In the ground squirrel, Michael (1967) reports that 45% of the tectal units are superficially located directional types like those of the optic nerve. No directional units have been reported in the Rhesus monkey (Humphrey, 1968) or baboon (Vejbaesya, 1967) but the latter study was not extensive.

The quadrant fields of the deeper regions of the rabbit colliculus have also been observed in the pigeon (by the author and by Bilge, 1967) and in monkey (Humphrey, 1968).

The units below the stratum opticum or incoming retinal fibres in frog, pigeon, rabbit, rat, monkey and cat have been reported to show habituation and in most cases the spontaneous disappearance and return of portions of the receptive field is common during examination. The receptive fields of the deeper regions of the tectum show, in all animals investigated, an extremely marked preference for moving stimuli rather than for stationary light spots.

ORIGIN OF COLLICULAR UNIT PROPERTIES

Many puzzles remain in the comparative physiology of the tectal single units in spite of the similarities apparent in the layering of unit properties in different species. One major problem is related to the identification of the extent to which the tectal unit population represents a direct retinal projection, collicular convergence or a projection from one region or another of the visual cortex. The problem is well exemplified by the case /

case of the directional unit. The subsequent considerations cannot, however, be carried far because many reports in the literature are perfunctory and probably do not represent the true nature of the collicular population of units. It is simply intended to reveal the incongruities of the results; clarification must await further experiments.

Directional units have not been reported to exist in the retina or tectum of frog, rat or monkey. They have been reported in the retina and tectum of the rabbit, ground squirrel and cat and have also been observed in the brachium of the superior colliculus of the rabbit and ground squirrel. The apparently straightforward conclusion that, if the units are present in the retina they project to the superior colliculus is disturbed by the percentage population reported in the various mammals. The cat retina appears to contain only 2% (Stone & Fabian, 1966) of directional units compared with 23% in the ground squirrel and 10-30% in the rabbit. In contrast, the cat tectum has been reported to contain 78% of directional units by Straschill and Tahavy (1967) and 64% by McIlwain and Buser (1968). Vejbaesya (1967) has reported a lower figure of 14% directional units in the colliculus of the cat and this might just be regarded as compatible with the percentage found in the retina if all the directional units passed to the colliculus. There is no basis, however, for the neglect of the findings of the other two sets of investigators. It thus appears that there is the possibility that the directionally selective units of the cat tectum are formed in that organ. Both direct projection from the retina and formation within the tectum may occur for different populations in view of Vejbaesya's (1967) report of superficial and deep directional units possessing different properties.

A further possibility for the origin of the tectal directional units remains, however, because in all of the mammals studied there is anatomical or physiological evidence for projections from VI and VII to the superior colliculus and some or all of the tectal directional units may arise at cortical level. The evidence is conflicting. In rat and rabbit the properties of the collicular units do not appear to change markedly upon removal /

removal of the striate cortex but in the former case directional units have not been observed while, in the latter, the directional units of the stratum opticum are still found after removal of the cortex but the directional properties of the deeper units, which are very difficult to study because of the time varying response, have not been assessed under such conditions. There is also the possibility that the cortex was not in good working order when the units of the supposedly normal colliculus have been examined although, in the case of the rabbit, many functioning units have been observed in passing the electrode through the visual cortex towards the superior colliculus.

According to Vejbaesya (1967) the upper tectal directional units of the cat do not disappear upon cooling the corresponding region of the visual cortex. Marchiafava and Pepeu (1966) describe the cat collicular unit activity as unchanged after neocortex removal. On the other hand, Wickelgren and Sterling (1967) report that the directional and orientation selective units of the cat superior colliculus disappear upon removal of the visual cortex and do not reappear even three weeks after operation. In contrast to the case of the directional units, Vejbaesya's results from cortical cooling during recording from the appropriate region of the colliculus indicate that the tectal orientation units result from a cortical projection and in this respect confirm the finding of Wickelgren et al. At present, no decision about the origin of the cat directional units - which may be multiple even for one cell of the tectum - can be reached.

Recent work by Michael (1967; 1968) has indicated the probability of a retinal origin for the tectal directional units of the ground squirrel. He has pointed out that 45% of the ground squirrel tectal cells as well as many of the optic tract terminals, are directionally selective. Because the LGN is free of directionally selective cells, he suggests that the majority of directional units project directly to the tectum in this animal. Orientation selective units, local edge detectors and uniformity detectors are quite common in the superior colliculus of the ground squirrel and are found /

found in the optic nerve but are not reported from the LGN. It is thus implied that these units - like the directional type - project directly to the colliculus.

The evidence from the ground squirrel, which is published only in preliminary form and is unconfirmed, thus suggests that the cortex receives only concentric and colour units and that the other unit classes pass directly to the tectum as a 'Key feature system' which was brought up earlier (p. 196). The hypothesis was rejected as not being of universal application because the orientation and directional units of the rabbit cortex are found to be almost identical to those of the retina and, although only directional cells have been recorded in the rabbit LGN, are unlikely to have been formed 'de novo' from concentric units at the cortical level while the retinal non-concentric units pass directly to the midbrain.

It is clear that more detailed - and quantitative - examination of the units at the different levels of the visual system is required for the elucidation of the above problems. The work must be directed towards the elucidation of criteria for the determination of the unit projections and the answer cannot be expected to arise from general surveys of the unit properties at different parts of the visual system. It is possible that the most direct results will be obtained by intracellular recording so that the receptive field of a unit and of the epsp or ipsp's generated by the units projecting to the cell may be determined.

SUMMARY

Ablation and single unit studies have indicated that, in a variety of mammals ranging from the rabbit to the monkey, the superior colliculus provides at least part of the mechanism for visual orientating and tracking responses. The degree of autonomy of the organ must depend upon the extent of development of the geniculo-striate system in different animals so that any general hypothesis of the function of the cortical projection must be regarded with caution. It must suffice to say that the colliculus may be regarded /

regarded as providing the control or 'error' signal which is introduced into the eye and head vestibular stabilising mechanism (Whitteridge, 1959) in order to counteract movements of the whole visual field or induce tracking of smaller objects. The visual cortex may be regarded as the pattern analysing and recognition system which uses the cortico-tectal pathway as a means for 'locking' the collicular system on to one target while leaving sufficient independence of function for the tectum to fulfil its function of an early warning system for the notification of novel activity within the visual field. This last function presupposes some degree of ascending projection from the colliculus and in this regard it would be of considerable interest to know whether the tectal projections to the reticular formation retain a topographic organisation. At present it is impossible to make any suggestion as to the reason for the double projection from VI and VII to the tectum because so little comparative information is available about the nature of the units in these cortical areas and in the deeper, neglected, regions of the superior colliculus where the cortical projections terminate and the properties of the movement sensitive units are so difficult to classify.

VISUAL CORTEX

ORGANIZATION OF SINGLE UNITS IN CAT VISUAL CORTEX

Thought about visual cortex organization has been dominated by the work of Hubel and Wiesel on the cat, (Hubel & Wiesel, 1959; 1962; 1965). Discussion of cortical organization must be prefaced by a summary of their findings because it is tacitly assumed by many workers that all other mammals will conform to the pattern revealed in the cat.

The single units of the retina and LGN are all identified as concentric types. The major population of VI is described as consisting of 'simple' units which require as stimuli a light or dark bar or in some cases an edge at some specific position and orientation. The adequate stimulus for these units may be predicted by an examination of the responses of the unit to a small light spot flashed at various points in the receptive field. Other cells, called 'complex', respond to appropriately orientated stimuli wherever it is situated within a receptive field which cannot be mapped out with a light spot. In VII, another population of cells termed low order hypercomplex units were discovered (1965) which respond to a slit, edge or bar which must be limited at one or both ends. In VIII even more complex behaviour was found in that 'high order hypercomplex units' would respond to a stopped line in either of two perpendicular orientations at any point within the receptive field. The percentage of the different types of unit occurring in the various regions of visual cortex is shown below (Hubel & Wiesel, 1965).

VI	75% simple 25% complex
VII	90% complex (large field) 10% hypercomplex
VIII	42% complex 47% low order hypercomplex 11% high order hypercomplex

No cells with concentric or circular field were encountered at cortical level.

Hubel and Wiesel (1965) instituted the hierarchical concept of visual cortex unit organization when they showed that the properties of simple units /

units could be accounted for by the convergence of geniculate axons on to a cortical cell in order to increase stimulus specificity, complex units by the convergence of simple unit projections, low order hypercomplex units by the convergence of complex projections and the high order type by the convergence of low order hypercomplex projections. This scheme was purely theoretical but was suggested by other findings.

In the early stages of their work, Hubel and Wiesel observed that all of the cells encountered during a single penetration might often possess similar or systematically changing orientation selectivity and stimulus requirements. It was also noted that penetrations over an area of 0.5 mm. in diameter would record cells with similar properties from top to bottom of the grey matter. Such regions were called 'columns' (Hubel and Wiesel, 1963). Within such columns of VI both simple and complex units were to be found with the same orientation and stimulus requirements. Similar columns containing the appropriate complex and hypercomplex units were recorded in VII and VIII. This arrangement would be economical for the organization of interconnections if their suggestions as to the origin of the more sophisticated unit properties were correct.

Hubel and Wiesel also demonstrated that area 17 projects to areas 18 and 19 so that an anatomical basis was found for the suggestion that the population of complex units in VII and VIII arose from projections of VI, either in the form of complex unit axons or simple unit axons, which converged to generate complex cells in VII and VIII. These concepts along with progressive increase in the percentage of sophisticated units in passing from VI to VIII led to the general acceptance of an hierarchical functional organization of the three cortical visual areas. Recently, however, several findings have come to light which suggest that the story revealed by Hubel and Wiesel has been over-simplified, as, of course, they have cautioned since its inception. These findings have not yet been absorbed into current thought on visual organization and will thus be listed before their discussion.

1. /

1. Retinal units of the non-concentric type have been described by a number of separate workers in the cat (p. 18 /). Units of more sophisticated function than the concentric form have also been recorded from the LGN of the same animal (Kozak, Rodieck & Bishop, 1964). These findings have not been commented upon by Hubel and Wiesel as late as 1968.

2. Recent work on the cat LGN has revealed that the main part of the nucleus projects topographically to VI and VII while the medial interlaminar nucleus projects to VIII (Wilson & Cragg, 1967; Garey & Powell, 1967). The small cells of the LGN appear to project to area 17 alone while the large cells project to areas 17 and 18.

3. In a recent paper on the monkey striate cortex, Hubel and Wiesel (1968) have announced that 20% of the cells in visual I of the monkey are hypercomplex and that, contrary to the previous report (1965), a somewhat lesser proportion of such units is to be found in the same area of the cat.

There are thus three separate populations of units projecting from the retina to VI, VI and VII, and to VIII. The discovery of non-concentric units in the retina gives rise to the possibility that these populations have different properties determined at the pregeniculate level. Now, in spite of the fact that no single units below cortical level have been described by any worker as being of other than 'simple' type, we find that Hubel and Wiesel (1965) state -

"Outside of VI no simple cells were found, and no axons with geniculate properties were encountered in the grey matter."

We thus must wonder as to the nature of the units projecting from the LGN and interlaminar nucleus to the areas VII and VIII. Are complex types formed from the geniculate projection within these areas? If so, why have the axons with 'simple' properties been missed? If not, are there complex units at the geniculate level which have remained unobserved?

The presence of hypercomplex units in VI may readily be accommodated within the column concept. Their presence may simply mean that convergence has occurred at an earlier stage than was assumed previously. On the other /

other hand, the small population of VI hypercomplex units may result from the convergence of the more sophisticated units ascending from the retina. Wilson's (1968) report of a projection from VII/VIII to VI opens up the further possibility that these units arise at a later stage and are fed back to VI. The discovery of hypercomplex units in VI obviously calls into question the reliability of the percentage of different types in VII and VIII in the 1965 paper.

The recent findings do not much affect the hierarchical concept of single unit synthesis at cortical level. It must not, however, be thought that the output of a given cortical region consists only of the axons of the most sophisticated cells of that area. In the corpus callosum of the cat the axons from VI contain simple, complex and hypercomplex units (Hubel & Wiesel, 1967) so that there is evidence of outputs from the intermediate stages of information processing, i.e. simple and complex units project rather than the hypercomplex units alone. The independent retinal projection to VII and VIII and the presence of feedback from VII/VIII to VI does, however, prevent the acceptance of the straightforward hierarchical concept of the roles of VI, VII and VIII as successive stages in the analysis of the visual image, each stage carrying out a more complex process than its predecessor. It is ~~was~~ apparent that there is a marked degree of parallel processing; each area has its own, individual afferent and efferent projection to other regions of the brain. The presence of independent projections from VI and from VII to the superior colliculus is indicative of a degree of functional autonomy for these cortical areas.

ORGANIZATION OF VI IN THE RABBIT

The striate cortex of the monkey has recently been shown to be very similar in its organization to that of the cat (Hubel & Wiesel, 1968). The same columnar organization of simple, complex and hypercomplex units is found in both animals although the stimulus requirements are somewhat more specific and the lamination of function is more clearly organized in monkey than that in /

in the cat. The limited data available (Marg, Adams & Rutkin, 1968) suggests that the human striate cortex may be organized in similar fashion.

It is consequently of considerable interest that our results indicate that the organization of the rabbit visual cortex differs very considerably from that of cat and monkey. Certain major points stand out -

1. In a given radially orientated slab, the unit properties encountered are different and are correlated to some extent with depth.

2. There is no evidence for either ordered or disordered columns such as are to be found in the cat or monkey.

3. The single unit population of the rabbit area 17 is in some cases, directional and orientation units, apparently very similar to the retinal units. The receptive fields are somewhat larger which indicates some convergence. It is possible, in the case of the evidence presented above, to suggest that these units are geniculate axons but Creuzfeldt has indicated in personal communication that a similar population of cortical cells is obtained by intracellular recording under which conditions confusion of cell and axon is not likely.

4. The edge, bar and orientation sensitive units exist in the rabbit area 17 but do not form the entire population as they do in the monkey and cat because there are many units with circular fields which are responsive to a wide variety of stimuli. The deep very large field units have no parallel in the cat and are most definitely cells in the deeper parts of the rabbit visual cortex.

5. A very large proportion of rabbit cortical units from layers II-VI possess 'simple' fields.

Although only the results of a preliminary investigation of the rabbit area 17 are available it is clear that the difference in organization of the rabbit and cat visual systems which is apparent at the retinal level increases considerably when the organization of units in VI is considered. Must the rabbit be regarded the possessor of a visual system organized at unit level in a completely different fashion to that of cat and monkey? The unit properties /

properties so far revealed do not suggest an hierarchical organization of the rabbit cortical units after the fashion of the cat and monkey although more detailed study may reveal such an arrangement. It appears that, in the cat and monkey, the topographical projection of the visual field breaks down at the cortical micro-level to the multiple representation of a given region of visual field which is necessitated by the mosaic of functionally dissimilar columns. In the rabbit, however, this does not happen in area 17 and the radial fasciculi^c apparent in histological sections of the visual cortex may be regarded as the possible basis of a functional module and as determining the ultimate resolution of the cortical map. In this respect the organization of the rabbit visual cortex appears to resemble that of the tectum rather than that of the cat visual cortex.

Obviously an important step must be the analysis of the single unit properties of the rabbit VII. Will this region reveal similar organization to VI or will units of more sophisticated function be revealed and found to be related in some hierarchical fashion to those of VI? All attempts at recording units from VII of the rabbit have failed although evoked potentials have been obtained which, like those of VII in the cat, possess a receptive field which is much larger than those of VI.

More information from the rabbit will not, however, alone be adequate to clear up the problems introduced above for it must be decided whether the rabbit is an unusual, specialised, animal or whether it is representative of the lower mammals. Little comparative data is available. The ground squirrel cortex has not been examined. All that can be said is that the rat visual cortex appears to be somewhat similar to that of the rabbit although much less sophisticated in its requirements for adequate stimuli (N. Block, personal communication).

STRUCTURE AND FUNCTION IN THE VISUAL CORTEX

There is little evidence of histological differences between the visual cortex of the rabbit and cat which might reflect the functional differences /

differences observed electrophysiologically. The most obvious contrast between area 17 in the two animals is related to the mode of termination of the afferent LGN fibres. These project to the layer IV and to the immediately adjacent layer III in the cat but to both layer IV and all of layer III in the rabbit. Globus and Schiebel (1967) have examined the literature on the site of termination of such fibres and find it assumed in the accounts of Cajal (1911), Lorente de Nó (1922) and O'Leary (1941) that the optic afferents mainly contact the short axon stellate cells which are so plentiful in layer IV. The stellate cells of layer IV in the rabbit are of more complex form and much lesser concentration than those of the cat or monkey (Beritoff, 1965); it is thus of interest to find that Globus and Schiebel report that the apical dendrites of the pyramidal cells receive a considerable direct projection from the LGN fibres in the layers III and IV of the rabbit. The stellate cells of layer IV may also receive a parallel input from the LGN in this animal. A detailed investigation of the organisation of the input in other animals has not yet been published but it appears likely that the classically assumed projection to the short axon stellate cells, although not yet histologically established, may play a greater role in the cat and monkey. In passing from the rabbit to the monkey, the potential monosynaptic cortical through-path, from the afferent LGN fibres to the apical dendrites of the cortical pyramids of layers V and VI and thence out of the cortex, may become replaced by, or less important than, a minimum path involving the stellate cells as interneurons.

Units giving a clear and reproducible response to the flashing of a small light spot are numerous in all layers from II-VI of the rabbit visual cortex. Spots of light evoke little or no response from the complex and hypercomplex units of the cat and monkey so that the responsive class is represented only by the 'simple' units in these animals. In the cat, the simple fields are confined to the very bottom of III, IV and VI (Hubel & Wiesel, 1962). This state is intermediate between that of the rabbit and the monkey in which the simple units are located in lower III and IV alone.

If /

If the disappearance of light spot responsiveness is a function of the number of synapses intervening between the recorded cell and the afferent fibres then it is possible to explain the above differences. In the rabbit, the widespread distribution of afferent fibres in layer IV and III coupled with the connection of afferents to the apical dendrites of cells in layers V and VI provides an anatomical basis for encountering units only one step removed from the afferent fibres in all laminae of the visual cortex. The widespread distribution of units responsive to light spots would thus be accounted for. In the monkey, if the afferents terminate on the stellate cells alone, the cells in direct contact with afferent fibres would only be found in the lower part of layers III and in IV where the stellate cell density is greatest (zone III of Sholl, 1955). Such a distribution is exactly that which is found for the simple units in monkey. It has not yet, however, been demonstrated that the LGN afferent fibres do not terminate on the apical dendrites of pyramidal cells in the monkey.

The first attempt to correlate the shape of the dendritic tree with the receptive field of the cortical units was made by Colonnier (1964). The basal dendrites of pyramidal cells and the dendritic trees of stellate cells in the cat cortex were examined in section tangential to the cortical surface and thus parallel to the plane of the visual field projection map on the cortical surface. Some of the pyramidal cell and most of the stellate cell trees were found to be oval or elongated in shape which Colonnier has suggested to be the anatomical basis for the ovality of the majority of the simple receptive fields. Certain facts argue against the significance of this correlation.

1. The shape of the stellate cell dendritic fields would only be imagined to be a significant feature in determining the form of the receptive field if the LGN fibres project up to the cortex in a rigid topographical array with which the cells may connect up. Since, however, the incoming LGN fibres may branch more than twelve times and spread over an area 1 mm. in diameter (Sholl, 1954) then the topographic projection must be blurred at this /

this level and a more specific basis for the formation of connections is likely in which case the spatial distribution of the dendrites will be irrelevant since they cannot enter into a uniquely determined relation with the incoming LGN fibres on the basis of their cortical coordinates alone.

It is of interest to note that the wide spatial distribution of the terminals of single LGN fibres is to be expected in the cat as a result of the presence of the cortical columnar organization because this requires that a given region of retina should project to a variety of functional columns. O'Leary (1941) has commented that the LGN fibre terminal distribution in the rabbit visual cortex is much more restricted than that of the cat. This is the opposite to what would be expected on the basis of behaviourally determined visual resolution but would fit in which the apparent absence of columns in the rabbit cortex which eliminated the need for extensive terminal branching. These considerations must remain little more than speculation until detailed quantitative description can be made of tissue from specified regions of the visual cortex in the different species.

2. The oval dendritic trees of the stellate cells are claimed by Colonnier to have a preferred orientation along the vertical meridian (1964). According to Hubel and Wiesel (1962) the simple fields have no preferred orientation in the cat.

3. Oval dendritic trees are not limited to the visual cortex and have been observed in all three auditory areas of the cat (Wong, 1967); they may be a general feature of the stellate neurons, although not of the pyramidal cell basal dendrites.

No work such as that of Colonnier has been carried out on the rabbit visual cortex in which the differential magnification along vertical and horizontal means that in some parts of cortex an oval dendritic tree might represent a circular receptive field and vice versa. An alternative method of correlating structure and function in this animal was suggested by the presence of the characteristic 10-30° diameter very large field units in layers V and VI which it was felt might be represented by correspondingly large /

large dendritic trees. Globus and Scheibel (1967) have, however, found that the basal dendritic skirt of the pyramidal cells, which must represent the very large field units of the deep cortex, shows little variation in diameter from layer II to layer VI of the visual cortex in rabbit. The mean diameter is 130 μ and there is no more than a 10% variation in this value. Thus, even if they examined the most compressed part of the cortical representation of the visual field (when Mv and Mh may be assumed equal at 0.05mm/ $^{\circ}$), the pyramidal cell skirt dendrites would represent a receptive field of no more than 2-3 $^{\circ}$ diameter. The diagrams of O'Leary and Bishop (1938) reveal larger pyramidal cells but the dendritic skirt of these is only about 0.4 mm. in diameter and they represent a receptive field only 10 $^{\circ}$ across which is still not adequate. It is unlikely that shrinkage during preparation would account for such a divergence. In view of the recent discovery that the LGN afferents appear to terminate predominantly on the apical dendrites of the pyramidal cells, it is unlikely that attempts to correlate the unit receptive field with the dendritic skirt would prove successful.

HOMOLOGY OF VII IN MAMMALS

In an earlier section it has been reported that the area 17 and area occipitalis of the rabbit correspond in location to VI and VII as has been found to be the case for the cat areas VI/17, VII/18 and VIII/19. There is no problem in establishing the homology of area 17 in the various mammals but the relationship of the rabbit area occipitalis, area 18a in the rat, and areas 18 and 19 in the cat and monkey, is much less clear.

The area occipitalis of the rabbit and area 18 of the cat are similar in that they both receive a transcallosal projection and bear a representation of the visual field (VII) which is a mirror image of that in the primary visual area. In the cat and rabbit, the densest callosal projection is to a narrow strip running along the VI/VII border. The transition from VII/VIII, or 18-19 does not receive such a callosal projection in the cat but /

but the lateral border of VIII is supplied by such fibres which lie in two bands or 'fingers' which spread out from the central region of the 17/18 border (fig. 109). No signs of such 'finger 18' have been seen in the rabbit but the lateral border of VII has not been identified electrophysiologically and nothing is known about its topography. Although the cytoarchitectonic evidence does not suggest the presence of an area VIII in the rabbit, there is thus no positive indication of its absence. Indeed, it has been shown in the section on the LGN that the rabbit possesses a second representation of the visual field in the LGN. If the organization is similar to that of the cat then this representation may be equivalent to the medial interlaminar nucleus of the cat which projects to VIII (Garey & Powell, 1968). The second representation of the visual field in the rabbit LGN may thus indicate the presence of an area VIII in that animal. The puzzle as to whether the cat and rabbit differ may simply result from the difficulty of access to the location of the rabbit VIII.

The arrangement in the monkey (*macaca*) has recently been outlined by Myers (1962; 1965) who found the borders of Brodman's area 18 to coincide with those of the transcallosal degeneration induced by removal of the opposite occipital lobe. His schemata is presented in fig. 109. The topography of the map is seen to differ from that of the cat only in that area 19 is shown as being present, 'area 19 proper', beyond the limits of 'finger 18'.

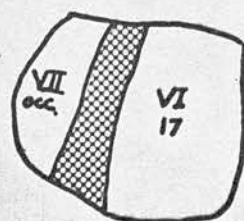
An examination of the literature on the electrophysiology of the monkey visual cortex reveals a dearth of material. Myers' work does help, however, in the interpretation of the results of Cowey (1965). In both rhesus and squirrel monkey, this author mapped out VI and VII. VI corresponded with area 17 but VII was found to be split into two components, one for the upper and another for the lower visual field. Unfortunately, Cowey specified no more than the fact that the VII representation lay in the pre-striate cortex. Examination of the relevant diagrams reveals that Cowey's VII corresponds well with the two regions of striate receptive 19 of Myers' /

Myers' scheme and not with area 18 as in the cat. As VI and VII of the monkey abut, there does not appear to be room for a further representation of the visual field on juxtastriate 18. In view of the problems associated with the delineation of cytoarchitectonic regions it would appear likely that the region of striate receptive 19 is incorrectly identified and in fact corresponds to the area 18 of other mammals. The general tendency in the series rat, rabbit, cat is for the callosal terminations to occupy more and more narrow portions of the area VII at the VI/VII boundary and it is odd that this should be reversed in the case of the monkey where, if Myers' terminology is accepted, the area of callosal terminations is equated with, not a portion, but all of area 18. Such a view appears to be held by Hubel and Wiesel (1965) who refer to unpublished work on the spider monkey in which they claim that VII lies in area 18 in similar fashion to the arrangement in the cat.

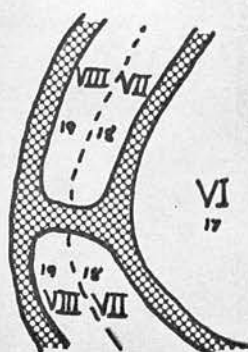
Even if the monkey striate receptive 19 is found to correspond area 18, the homologies of the monkey visual areas would remain obscure. Myers has specified that the regions of area 17 near to the projection of the horizontal project to the far limits of striate receptive 19 while areas near to the border with juxtastriate 18 project for only a short distance into striate receptive 19. Such an arrangement indicates that, in the monkey, the areas lying between the ⁺juxtastriate 18 and finger 18 (area 18 proper) bear only one representation of the visual field which would correspond to the two components of Cowey's VII. In the cat, this region contains both VII and VIII. If VIII in the monkey corresponds to the area 19 proper, which lies outside finger 18, then the arrangement is very different to that of the cat.

A further difference between the monkey and cat VI lies in Cowey's demonstration that the second visual area is maintained, in the squirrel monkey, by projections from VI. Talbot (1942) and Doty (1958) have shown that the cat VII is still demonstrated in the absence of VI. The projections from the LGN to VII in the cat which pass directly to VII and provide the /

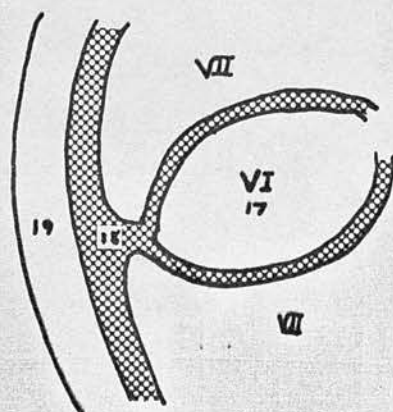
Fig. 109 Topology of the visual areas in rabbit, cat and monkey. See pages 254-257. Not to scale.



RABBIT



CAT



MONKEY

the basis for their findings have already been described. As the rabbit visual area defined on the basis of a geniculo-cortical projections by Rose and Malis (1965) extends laterally into the area occipitalis, it would appear that the situation with regard to VII in the rabbit corresponds with that in the cat rather than the monkey and that the main LGN representation projects to VI and VII.

Until the lateral boundaries of VII in the rabbit have been explored electrophysiologically and the differences between cat and monkey have been cleared up, there can be no very profitable discussion of the homologies of the visual areas of rabbit and monkey and no prediction of the properties of the rabbit VII units may be made on the basis of what has been observed in the cat.

It might be expected that the study of the efferent connections of the cytoarchitectonic divisions of the occipital cortex would suffice to elucidate the homologies between species. The variation in topography of these areas in individual animals and of the criteria used by different investigators for the designation of the regions is, however, so great that the placing of lesions in areas other than 17 has rarely been discreet and overlap between 17/18 or 18/19 usually occurs. An attempt was made to obtain reliable data from the literature on the differential projection of the various regions of the visual cortex but a satisfactory set of data could not be collected and no attempt could be made to indicate the homologies of the regions on this basis.

LATERAL GENICULATE AND VISUAL CORTEX FUNCTION

No attempt has been made to include a discussion of the functional role of the LGN. It is known that the single unit properties at the input and output of this nucleus are similar to one another in both cat and rabbit. In the rabbit at least, however, the impression gained from recording within the nucleus is very confusing. The more detailed investigation of the geniculate cell properties which might reveal the function of the nucleus has /

has not been carried out while the significance of the LGN 'projection lines' and of the cortico-geniculate fibres (Szentagothai, Hamori & Tombol, 1966) which apparently contact the LGN neurons indiscriminately remains to be discovered.

In the section dealing with the superior colliculus some behavioural evidence relating to animals which had undergone various ablations was brought forward to indicate the role of that organ in visual orientation. The same work indicated that the striate cortex is an essential component in the mechanism of pattern recognition. A functional interpretation of the tectal single units was later attempted on the basis of the behavioural findings. No attempt at such a description of the role of cortical single units in pattern recognition can be made at present. Even the hypercomplex units of the cat and monkey are probably very early components in the process of abstracting complex information about form from the retinal image.

It must also be remembered that the results obtained by Hubel and Wiesel and the majority of other workers are from the lightly anaesthetised animal. Examination of the statistical behaviour of the visual cortex units in the unanaesthetised cat (Burns, 1968) suggests that the requirements for the excitation of a given cortical cell are less rigorous than is indicated by the results of Hubel and Wiesel. The optimum response is, however, only elicited by a very restricted variety of stimuli. The presence of any pattern in the visual field of a normal animal may thus elicit firing or inhibition in the majority of cortical cells and the interpretation of this activity must require statistical processes whose basis is far from clear. In view of our lack of knowledge about the principles governing the analysis of visual information, it is not possible to distinguish significant and insignificant differences between species. It thus remains to be seen whether the rabbit cortex works along completely different lines to that of the cat, or is fundamentally similar.

EXPERIMENTAL METHODS

PREPARATION OF ANIMALS

Anaesthesia. Pigmented rabbits were used for all experiments. The body weight ranged from 2.5-6 kg. For work on the colliculus or optic nerve the animal was anaesthetised by injecting 8 cc/kg. of 25% (by weight) solution of urethane in saline into the marginal vein of the ear. The animal will co-operate well if the ear is swabbed with ether before making the injection. If the injection was carried out quickly, it was found that respiration ceased abruptly. By the time recording began - some four hours later - it was usually found that the depth of anaesthesia was not great and brisk withdrawal of the paw occurred when it was squeezed. Anaesthesia was mainly by the very slow injection of 1 or 2 cc., of the urethane solution, while monitoring the activity of units in the region under study. When the animal was to be used for the study of cortical activity, the initial induction of anaesthesia was the same but maintenance was achieved by arranging that the animal inhaled ether vapour. A respiration pump sucked air through an "Oxford vaporiser", which may be set to give concentrations of ether vapour from 0 to 25%, and the ensuing mixture was supplied to the animal. If necessary, oxygen could be fed into the system but was found to be of little benefit.

Operative Procedure. After inductions of anaesthesia the eyes were examined by ophthalmoscope in order to detect any corneal opacities, cataracts or other features which would suggest the animal to be unsuitable. The eye-lids were rubbed together in order to stimulate the secretion of an oily fluid which helps to protect the cornea in the ensuing surgery (Arden, 1963). A thread was attached to each of the eye-lids and a lateral canthotomy carried out. A fine, curved eyeless ophthalmic needle was used to place four sutures through limbus; one at each pole. This procedure was applied only to the left eye. Afterwards the two eyes were closed.

A tracheal cannula was fitted and cleaned out at intervals by a feather.

The skin, connective tissue and cartilage of the external ear base were incised just in front of the bony ridge which is at the end of the external /

external auditory canal. A small opening was cut, about 1 cm. long, through the tissues until the canal was reached. If dissection is carried out carefully and with blunt instruments, it is possible to avoid all loss of blood at this stage. A careless incision placed nasal of the 'buttonhole' may sever one of a number of small arterial branches which will open when the animal is placed on the head holder and cause the loss of a great deal of blood. Wool plugs were placed in the openings in order to ensure their rapid location when fixing the animal into the head holder. If this is not done, swelling may obscure the opening and the ear pieces of the holder can be repeatedly inserted incorrectly.

The scalp was incised along the midline from a point at the base of the nasal bone to Lambda and the skull underneath thoroughly freed of muscle attachments and periosteum. Bleeding was stopped with plasticine. Muscle attachments were dissected away with a cautery. A trough was drilled, under microscopic control, in the skull around the area which it was intended to remove. Intermittent saline irrigation was used to prevent overheating. The drill bit was of the diamond studded variety and did not clog or stick during drilling. It was possible to observe the bone of the skull becoming transparent just before the burr bit~~was~~ through and drilling was stopped as soon as the blood vessels of the brain became visible. A thin scalpel blade was inserted, almost horizontally, into the trough and forced through. It is possible, then, to lever the circle of bone up from its position and break its continuity with the remainder of the skull. The dura remains intact and the brain surface completely unmarked.

The animal was wrapped in an electric blanket whose power supply is regulated by a rectal thermometer and a temperature set control and transferred to the head holder. The ear pieces were fitted, a mouth bar inserted and a nose clamp brought into position thus fixing the skull very firmly with Lambda some 1.5 mm. lower than Bregma according to the standard position of the atlas of Sawyer et al. (1954).

A 4% solution of highly purified and transparent 'Ionagar' was made up in saline and kept in a boiling water bath for some twenty minutes. The dura /

dura was incised with iris scissors after being lifted with watchmaker's forceps and reflected over the bony edges of the skull. When dry, the dura so placed retained the blood that sometimes issues forth from the skull boundary when warm agar was applied. The skin flaps of the scalp were sutured and tied back and some ridges of cotton wool soaked in agar were placed so as to build up a pool around the skull opening. The brain surface was gently cleared of C.S.F. and agar warmed to 42°C was poured on to it. If the skull was well dried, the fixation of the agar was excellent and the brain surface pulsations were quite eliminated.

Eye Fixation. The sutures which had been placed around limbus of the left eye were then fixed loosely to a brass ring. Under ophthalmoscopic observation the eye was manoeuvred into the standard position with the myelinated band horizontal and the optic disc on the vertical meridian projecting some twenty degrees down into the lower field. The sutures were tied permanently to the ring.

The refraction of the eye was assessed by direct ophthalmoscopy and a contact lens was chosen from a limited range of single curvature lenses originally constructed for human use. The corneal curvature of the rabbit falls into the range of human values. The animals were all within one diopter of emmetropia when fitted with plano lens of 7.6 mm. radius of curvature backed by a meniscus of buffered wetting solution. The main disadvantage of not using special lenses is that the rabbit eye has a much larger cornea than the human eye and the limited peripheral field with human contact lenses would prevent study of the binocular field .

STIMULATING AND RECORDING EQUIPMENT

Stimulating Equipment. A variety of means were used to present visual stimuli to the animal - neon flash, card stimuli, a projection perimeter and a special multi-purpose visual stimulator.

In both mapping and single unit experiments the visual field was explored with a small neon tube which was driven, by an EPI Dual Pulse Stimulator, to flash about once every two seconds. The neon provides a means /

means for roughly localising the receptive field of a unit or evoked potential. More precise location of the receptive field was then carried out by means of card stimuli mounted on short wands. The stimuli consisted of circles and bars of various sizes which were white on one side and black on the other. These figures could be presented against a background of white or black card. In the case of the more sophisticated units of retina and visual cortex it was often impossible to locate the unit receptive field by means of the neon and card figures were the only means of identifying the site of the receptive field.

Perimeter

For mapping experiments the eye was centred on an Airmark perimeter which can project a variety of small light spots of various intensity. In the absence of a neutral density filter, the brightness of the projected spot is about 40.0 cd/m^2 . The device is provided with a shutter behind which a OCP71 transistor photocell was placed. The output of the photocell provided a monitor signal which could be displayed under the record of unit activity and arranged to provide synchronising trigger for the cathode ray tube sweep generator at on and at off of the light spot. The perimeter is provided with a device which punches the coordinates of the receptive field upon a card which may be kept as a record of the experiment.

Multi-Purpose Visual Stimulator

The perimeter described above is not convenient for the detailed analysis of the properties of single units. For single unit experiments the animal was arranged in the head holder which was mounted on a dental chair base and could be rotated around its vertical axis. In front of the rabbit, at a distance of one metre, was placed a large steel sheet. When a single unit was recorded it was possible to move the animal around on its stand until the receptive field was centred on the screen. If this procedure was carried out slowly, it was possible to avoid loss of the unit.

A sheet of paper could be fastened to the steel screen with magnets so as to intersect the projection of the single unit receptive field in a plane tangential to a cylinder described about the posterior nodal point of the /

the eye and of radius one metre. Two photocells were also available, fastened to magnets so that they could be moved about the screen, ~~and~~ to record the passage of stimuli across their surface on the monitor trace of the oscilloscope.

Mounted on an old X-ray tube stand next to the animal was the multi-purpose visual stimulator which was arranged to project on-to the screen. The plan of this device is indicated in fig. 111 (Hughes, 1968).

Light from the quartz-iodine bulb is shuttered at S by an arm mounted on an electric motor driven between stops by a transistor bi-stable. The lens C acts as a condenser.

The aluminium disc D encloses three thin brass discs, 1, 2 and 3 (fig. 111b), each of which bears eight holes and may be rotated, by a finger applied at the notch N, about an axis R in order to bring any one hole into the position A which is at the object plane of the projection lens P. The patterns for projection are cut from aluminium foil stuck to cover glasses mounted in the holes of the brass discs. One hole in each disc was left empty. Discs 1 and 2 each contain one edge and six slits of varying width positioned along a diameter of the pattern hole. The patterns of discs 1 and 2 are orientated so that, when they are superimposed at A, the axis of bars or edges cross at right angles. These two discs give provision for projection of edges, corners and various squares, rectangles or tongues. Disc 3 bears selected patterns for the projection in black on a white background.

The projector assembly and disc D form one unit mounted in the ball bearing race BB₁. The projected images may thus be spun around their centre point by rotating the disc D.

The projection lens is followed by a front surfaced mirror, mounted on the coil of a moving-coil relay which may be driven by a time base or from a potentiometer. The projected image may thus be displaced along one axis of the screen at constant or variable velocity. The orientation of the stimulus pattern to the direction of movement is determined by the position of the disc D.

The /

The light finally passes through a Dove prism, DP, which may be rotated about its long axis and which consequently enables the projector axis of movement to be rotated about one point on the screen without interfering with the orientation of the patterns with respect to the direction of movement. The whole apparatus is mounted on a pan and tilt head.

The control system for the mirror drive enables selection of the starting point, distance and velocity of movement. If the apparatus is set up to present a given stimulus moving along one radius of a receptive field then the response along other radii may readily be determined under identical conditions by simply turning the Dove prism.

The pan and tilt head also bore a small Prado 150 watt projector whose beam was centred upon the same point as the multi-purpose stimulator. This projector was fitted with a 2 log. unit neutral density wedge, an iris diaphragm and could also accept slides. A camera shutter was fitted to the projection lens. The auxillary projector provided background illumination for card stimuli, or for generating shadows, as well as a continuously variable spot from 0.25-50° in diameter. Annuli could also be generated.

The beams of both projectors on the pan and tilt head provided monitor signals for scope display and the signal providing the moving coil relay power could also be monitored to give a continuous record of the movement of the stimuli.

Recording Equipment.

Micro-electrodes

Electrodes were of two kinds. The tungsten version was formed by electropolishing a 0.5 mm. tungsten wire which had been carefully examined for the purpose of eliminating samples showing signs of lamination. A very long taper was found to be most satisfactory in contrast to the blunt form described by Hubel (1957). It must be remembered, however, that his wire is initially much thinner than that used in these experiments. The electropolishing was carried out with 12 V A.C. applied between the electrode and a carbon rod both dipped into a saturated solution of sodium nitrite.

The /

The electrodes were dried, thoroughly washed in acetone and then dipped into a thin bakelite varnish with their points down. After removal they were inverted for 5 minutes and baked in a hot air blower furnace for another 5 minutes. The temperature was raised slowly in order to avoid blistering of the varnish. The dipping process was repeated three times and the electrodes were left to stand overnight.

The electrodes were inserted into the system shown in fig. 112 for testing. Current was passed through the electrode from a 1.5 V battery in series with a $2 \cdot 10^6$ ohm resistance until the pulse shape displayed on the oscilloscope was of the form pragmatically determined to be best for single unit isolation. The electrodes produced in this fashion are extremely uniform and reliable. Very few rejections are necessary if the terminal 'blasting' procedure is carried out with care. One electrode served in eight experiments over a period of one month and was still able to pick up well isolated units.

Fibres in the optic nerve were recorded by the use of glass micro-pipettes filled with Wood's metal. Thin capillary tubing was pulled to form glass microelectrodes with very fine tips. Under microscope control the tips of the electrodes were broken off by gently touching them against the edge of a microscope slide. The tips which were about $1-2 \mu$ in diameter were chosen. A small slug of Wood's metal was then inserted into the pipette and pushed along with a piece of straight copper wire. The tip of the pipette was held above a warm soldering iron until the Wood's metal had melted for part of its length and pressure was applied to the copper wire. The metal runs along the pipette and fills it leaving a small ball at the tip which is readily removed by vibration. The other end of the electrode was carefully warmed until the metal had melted and the copper wire was sealed into place. Before use the electrodes are plated with platinum black by making the electrode the cathode in a circuit containing a 1.5 V cell, a $2 \cdot 10^6$ ohm resistance and a carbon anode. The electrode and anode are dipped into a 1% solution of chloroplatinic acid, 0.01% lead acetate and 2 cc. of gelatin per 100 cc. of the main solution. A cap of platinum /

platinum black is observable when the electrode is checked under a microscope before use.

Apparatus. The microelectrode was carried by a simple micrometer drive, which has very low torque, for vertical movement. Two, more coarse, drives provided movements in the horizontal plane.

Evoked response and single unit activity were recorded as a potential developed between the electrode and a silver wire buried in the animal's neck muscles. The recording system initially consisted of a cathode follower, calibration box, Tektronix 124 preamplifier and power supply and a Tektronix 565 oscilloscope fitted with two 3A74 four trace amplifiers. Action potentials were made audible by an E.P.I. monitoring amplifier and loudspeaker.

Filming was initially carried out during the experiment with a departmentally constructed camera - later a Shackman 35 mm. camera was used. This procedure was found to be very time consuming and to detract from the study of the single units. It was thus arranged that any responses which might be desired on film should be tape recorded and filmed later, at leisure, during replay.

A Ferrograph two channel stereo tape recorder was selected. One channel was supplied with the unit activity from the 124 preamplifier and with the output of a microphone. The other channel simply carried monitor information from the photocells or visual stimulator mirror drive. As these signals may be of long duration with pronounced D.C. components, it was necessary to obtain an F.M. modulator and de-modulator for this channel.

The simple and economical design of Tempest and Bryan (1967) was used in modified form. The output stage of the original design requires inductive elements and the overall gain of the system is not unity. The modulator design remains unchanged from the original system. The de-modulator has been altered to incorporate capacitative filters (Hughes, 1968). In fig. 113, the component values are indicated only in the case of parts not present in the original design. The introduction of frequency doubling between the ⁷Schmitt trigger and the monostable, by the addition of a second trigger /

trigger diode, D, considerably improved the output signal to noise ratio. The output section, after the two stage taper filter, provides a means of pre-setting the output D.C. level, P.S.2, and for adjustment of the overall gain of the system to unity by variation of the feedback in the amplifying stage, P.S.1. The output signal is 3 dB down at 400 cycles and contains about 30 mV of carried noise which is independent of the input signal magnitude. The system is linear for inputs of ± 5 V. The input on the two channels feeding the recorder was displayed on one beam of the 565 C.R.O. and the output of the tape recorder on the other. The tape recorder was used instead of a written log of the experiment with relevant commentary being spoken into the microphone in between recording of unit properties.

HISTOLOGY

Golgi Retina. A modification of Polyak's rapid Golgi method was used (1941). The animal was anaesthetised with urethane and a small hole was made through the sclera, into the vitreous, with a thick hypodermic needle. Diametrically opposite this hole the same needle, connected to a 10 cc. syringe, was used to inject fixative into the vitreal cavity. The fixative consisted of

4 pts of 2% potassium dichromate
1 pt of 1% osmium tetroxide.

The injection was repeated; the eye was then removed and immersed in more fixative. After $\frac{1}{2}$ hour the front of the eye and lens were cut away and the cup was placed in fresh fixative for seven days at 37°C. The eye cup was then blotted dry and transferred to two changes of 1% silver nitrate solution at room temperature. After soaking for two days the orange precipitate was washed away. Dehydration was carried out in an incubator at 57°C in a mixture of 1/3 acetone and 2/3 absolute alcohol which had a few crystals of cupric sulphate added. The eye was then placed in fresh xylol, transferred directly into paraffin and blocked. The sections were cut at known orientation with the block surface warmed to prevent curling. The paraffin was removed under individual supervision by flooding the sections /

sections with xylol after they had been placed on warm slides bearing a thin layer of albumin. D.P.X. was used as a mounting medium.

In Vivo Methylene Blue Stained Retina. The dendritic pattern of ganglion and amacrine cells was readily displayed by the use of Polyak's vitreal cavity injection technique. The animal was anaesthetised with nembutal or urethane. A hole was made just below limbus through the sclera. Diametrically opposite to the hole a small 1 cc. hypodermic syringe fitted with a no. 18 needle was inserted as far as possible into the eye while lying in a plane parallel to the iris and just behind the lens, which must not be injured by its passage. The needle was slowly withdrawn as about 1.0cc. of 0.05% methylene blue solution was injected into the eye. During withdrawal, the needle was swung in a wide arc to break up the vitreous but care was taken to avoid damage to the retina. An ophthalmoscopic examination was then made to ensure that the dye had been uniformly distributed. The retina was left to stain for about 20 minutes.

The eye was rapidly removed; the sclera was cut around the limbus with fine pointed iris scissors and the whole front of the eye including the lens was lifted away. The eye cup was immersed in warm saline and turned inside out over the little finger. The thumb nail was used to hold down the choroid and then, while immersed under saline and viewed through a dissecting microscope, the retina was gently peeled away from the choroid by manipulation with small pads of cotton wool held in a pair of watchmaker's forceps. The optic nerve head was cut through. The retina was lifted out of the saline by bringing up a glass slide from underneath and passage through the water surface spread it flat with the vitreal surface uppermost. Several cuts were placed to enable the retina to lie flat. Bluing of the retina may then be observed in air. When the blue is adequately developed (looks quite pale), the retina is covered with a 10% solution of ammonium molybdate in distilled water to fix the stain. It was found best to place a cover glass on the retina at this stage in order to ensure a flat preparation. After about $\frac{1}{2}$ hour the preparation was washed in distilled water and transferred to a 10% solution; clearing and mounting followed. It was not found /

found to be necessary to cool the retina during tissue and stain fixation as is recommended by Polyak,

Whole Mount Retina Stained with Methylene Blue. For ganglion cell perikarya distribution counts and for perikarya diameter measurements the neurons were stained in vitro by methylene blue. The retina was removed without staining in the fashion described in the previous section, placed whole on a freshly gelatinised slide and cut to enable it to lie flat. The tissue was then placed in formalin for five minutes. The method subsequently followed that is described by Stone (1965) without deviation.

Optic Nerve and Retina Preparation for E.M. Work. The optic nerve and retina were fixed by an in vivo injection of a gluteraldehyde fixative after which the tissues were dissected out and transferred to an osmium tetroxide fixative for three hours. The procedure was exactly as described by Sjöstrand (1964, chapter 14, paragraphs 5, 6 and 7).

The retina was cut into identifiable strips and placed with the optic nerve into 75% ethanol for 30 min. followed by 100% ethanol for 2 hours. The tissues were then placed in a small plastic dish and covered with Araldite mixture for 1 hour at 57°C with one change. They were then transferred to fresh Araldite and polymerised at 57°C for 1 day and left to stand at room temperature for 24 hours before cutting on the ultramicrotome.

Once adequate sections had been obtained on the copper grids used for E.M. work, they were stained in a saturated solution of aqueous lead hydroxide for 1 hour before examination.

Routine Histology after Mapping Experiments. At the end of the experiment the rabbit was killed with an overdose of nembutal and perfused through the ascending aorta with a 10% solution of neutral formaldehyde, in saline. The next day, while the head remained in the head holder, the relevant section of brain was removed using a knife blade mounted in the micromanipulator to make the cuts in the necessary plane.

The sections were cut at 100 μ of the freezing microtome, mounted on slides coated with chrome-alum/gelatine solution and dried on a hot plate. After dehydration in alcohol the sections were stained with 1% toluidine blue /

blue for 15 minutes (Miehrome, Edward Gurr) and differentiated in Gotthard's differentiator. The sections were again dehydrated, cleared and mounted in D.P.X.

NOMOGRAPHIC TRANSFORMATION OF THE VISUAL FIELD COORDINATES

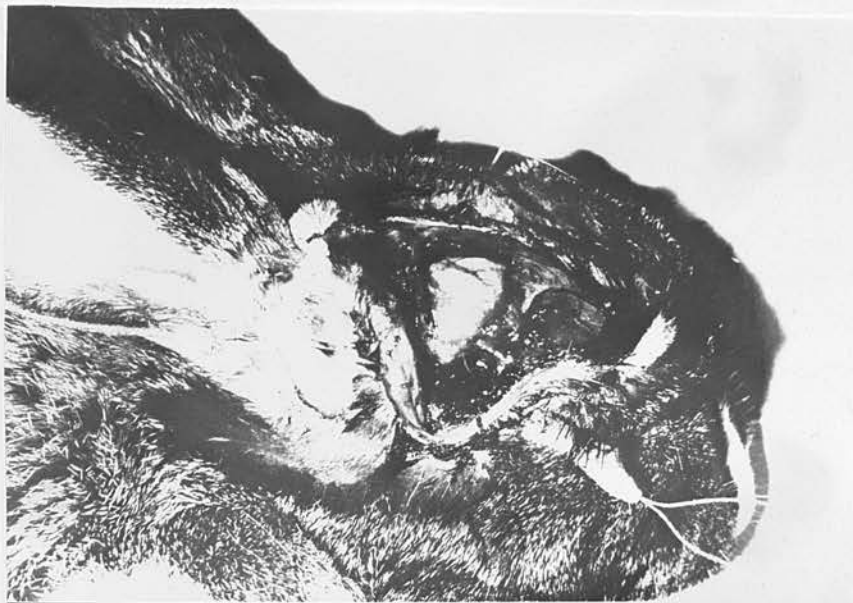
The eye position during mapping experiments was seldom exactly in conformity with the standard eye position in which the myelinated band is arranged to project parallel to the horizontal and the optic nerve head to be on the central vertical meridian and 20° below the projection of the centre of the coordinate system. In order to avoid a tedious calculation for each of the plotted points a nomographic technique was developed for transforming the coordinates recorded to those which would have obtained if the eye had been in the standard position. The opportunity of this transformation was taken to change the polar coordinate system of the perimeter to a system of parallels and meridia, the equatorial azimuthal orthographic projection, judged more suitable for an animal with an extended visual streak.

The receptive field coordinates for each point recorded in the brain along with the coordinates of the optic nerve head and myelinated band were marked on tracing paper overlying a plot of the polar azimuthal orthographic projection (fig. 114). The centre of the projection was marked on the paper. The equatorial plot (fig. 115) was then substituted for the polar plot with the centre coinciding with that marked on the tracing paper. The central parallel of the equatorial plot was arranged to intersect the optic nerve head position. A second fresh piece of tracing paper was pinned above the first and the centre marked. If the optic nerve head were read to be x° from the centre of the projection along the central parallel, then each point marked on the sandwiched, or first, piece of tracing paper was imagined to be moved x° along a line parallel to the central parallel and in the direction required to bring the optic nerve head from its original position to the centre of the projection. The distance of the move was read from the underlying grid and varies with the position in the field. The final point was marked on the upper piece of tracing paper. This upper sheet /

sheet thus represents the relative positions of the receptive fields if the eye had been arranged with the optic nerve head at the centre of the visual field coordinate system.

The middle tracing paper was then removed; the top tissue was rotated about its centre (i.e. the projection of the optic nerve head) to bring the projection of the myelinated band to a position overlying the vertical meridian. A new sheet of tracing paper was placed on top and each point on the middle sheet was moved 20° along a line parallel to the parallels; the distance was again read off from the underlying chart (fig. 115) and the final point was marked in on the upper sheet of tracing paper. The middle sheet of tracing paper was removed and the top one rotated through 90° to bring the projected points of the myelinated band into the position in which they run along the -20° parallel. The transformed coordinates of the various points could thus be read off from the projection grid.

The procedure appears to be complex but if the operations are sketched out, it will be seen that the principle is simple. The first process enables any deviation of the myelinated band and visual streak from parallelism to the horizon to be removed while the second process brings the optic nerve head down to the standard point at the intersection of the vertical meridian and the -20° parallel.



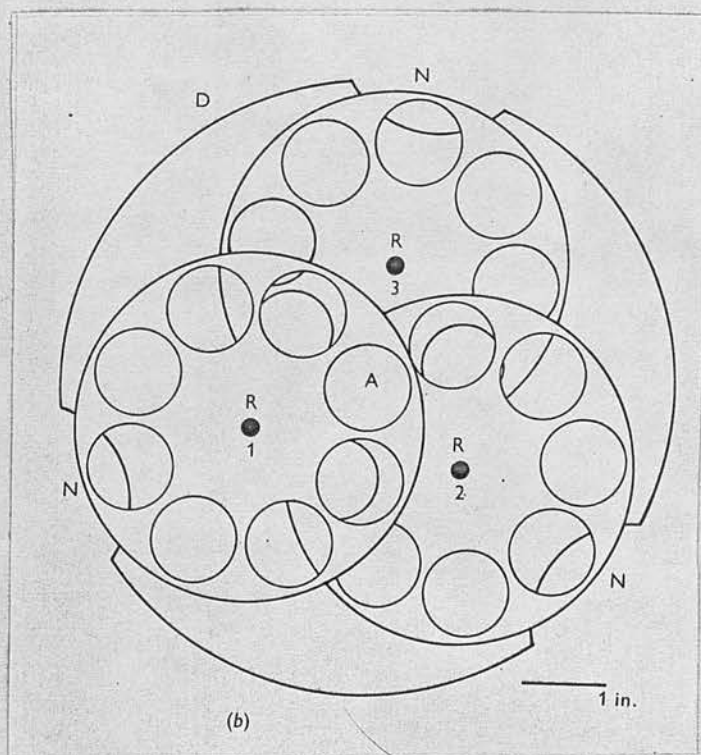
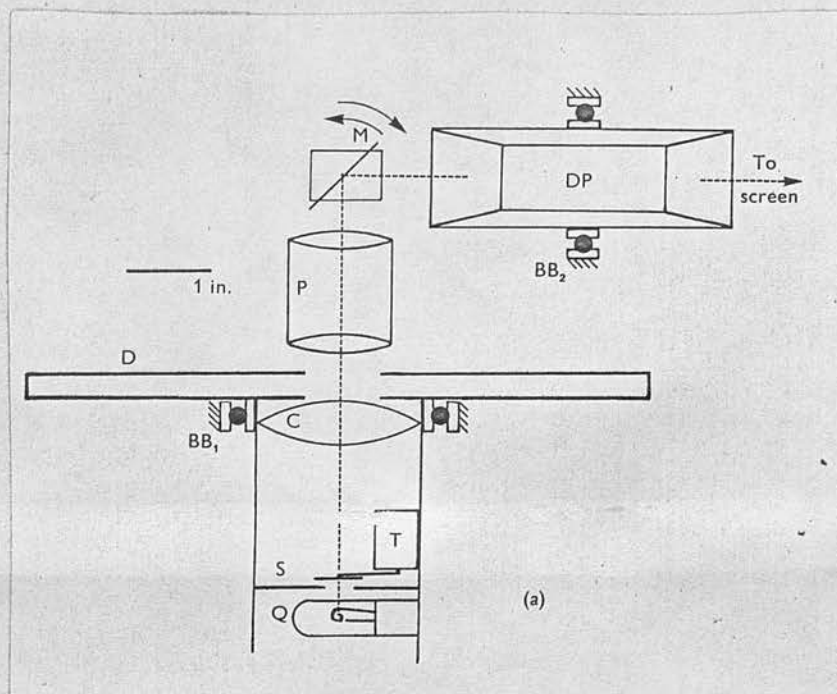
A



B



C



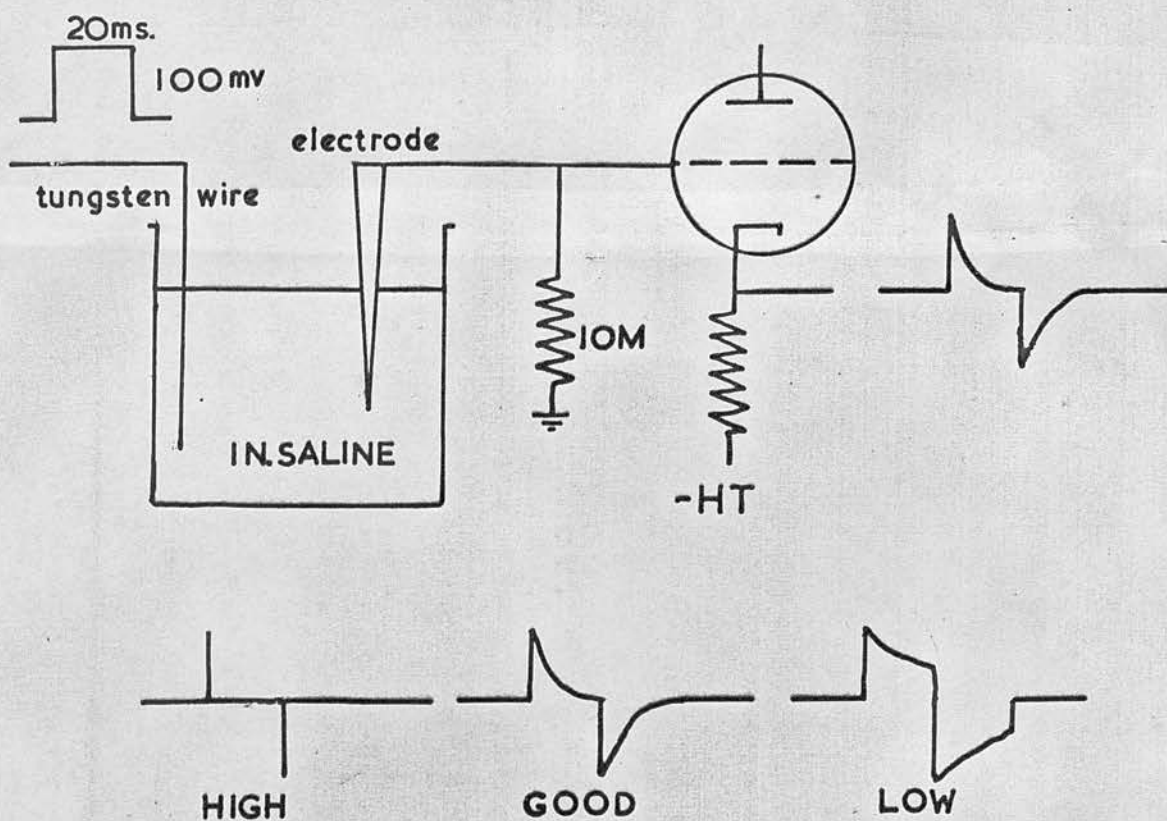


Fig. 11b Modified F.M. demodulator described on page 266.

Fig. 114 Polar azimuthal orthographic projection.

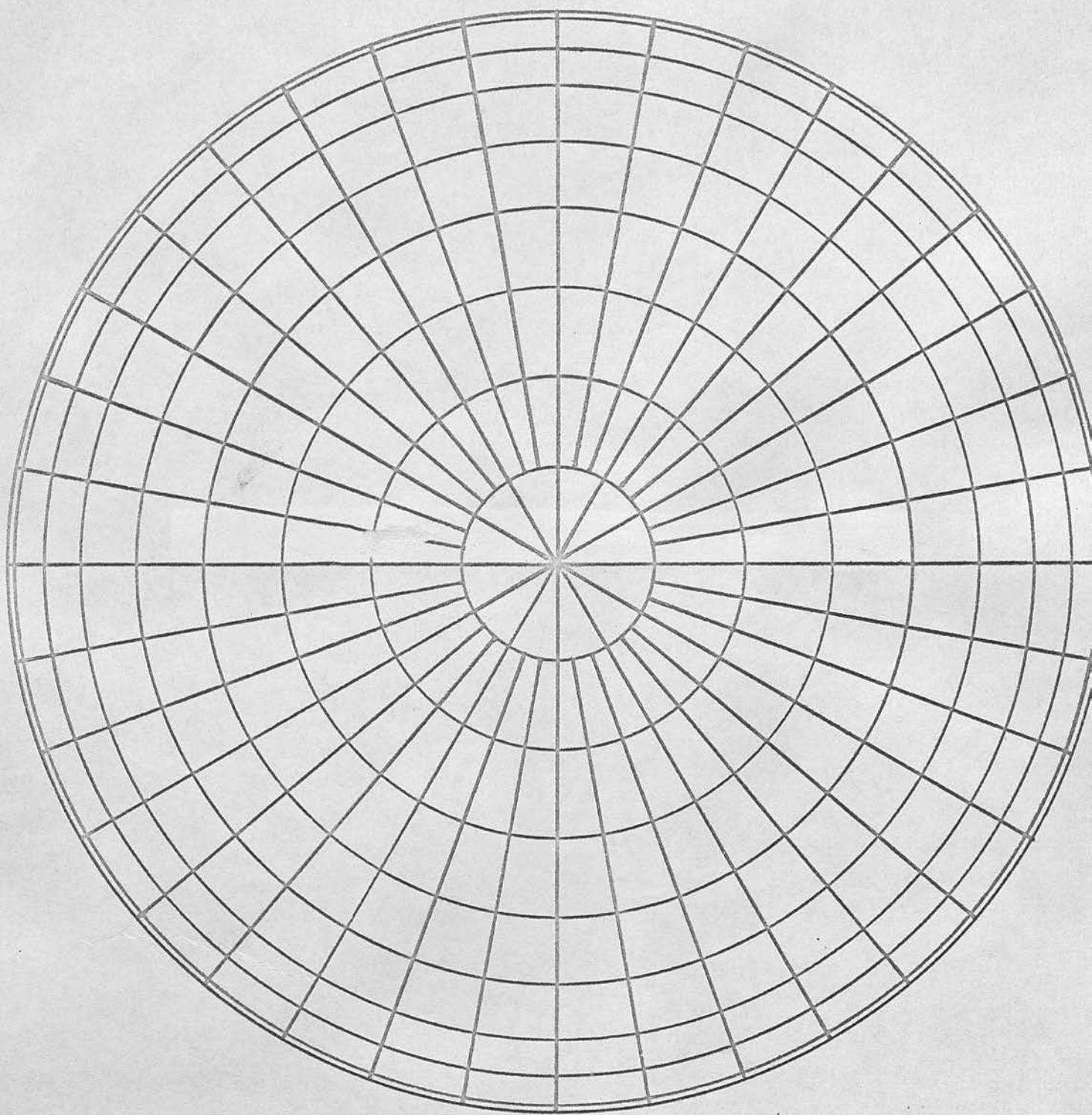
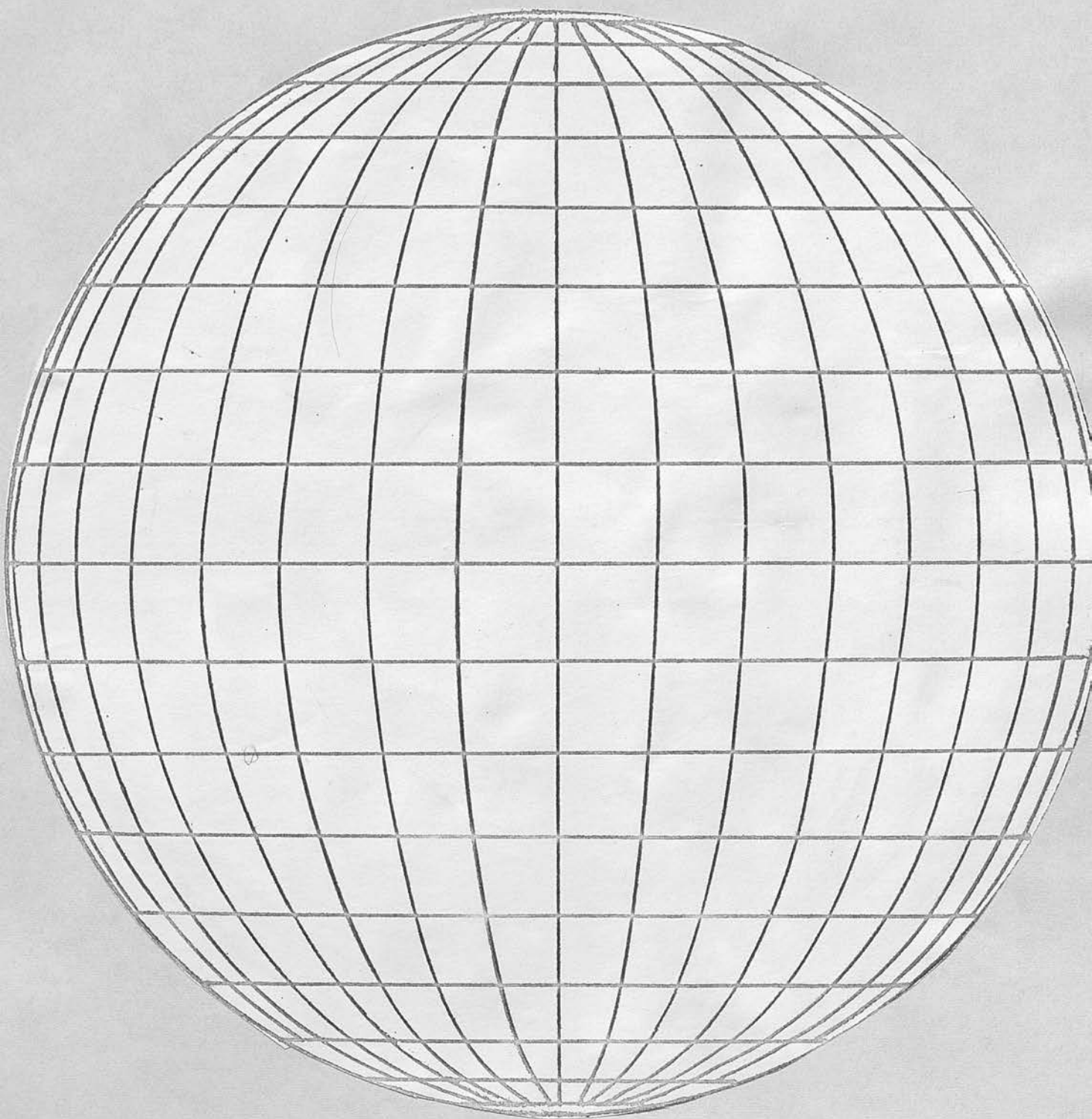


Fig. 115 Equatorial azimuthal orthographic projection.



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ABSTRACT OF THESIS

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Title of Thesis Studies on the Visual System of the Rabbit.

A schematic eye is developed for the rabbit and the arrangement of the eyes in the head is discussed in relation to the animal's field of view.

A detailed description of rabbit retinal histology is given which indicates the presence of atypical cones but, in spite of the specialised rabbit retinal units, an otherwise typical mammalian organisation. A quantitative description of ganglion cell density and size distribution is given which clearly illustrates the organisation of the visual streak. The visual streak is also shown to be represented in the bipolar and receptor layers of the retina. An optic nerve fibre count and axon diameter distribution are presented for comparison with the retinal data.

The topography of the projection of the visual field in the superior colliculus, L.G.N. and cortex is developed with one set of experimental techniques. Data is presented on magnification factor and volume representation for all three regions. The relationship of the form of the projection to the organisation of the retina is examined in discussion and a functional interpretation attempted. The differences between rabbit and cat central representation of the visual field are described and the concept of the rabbit as a parallel and the cat as a series visual data processing system is developed. The rabbit is shown to substitute head movements for voluntary eye movements.

The distribution of the callosal projections to the VI/VII border is given and the relation of the cortical visual areas to area 17 and occipitalis is indicated.

The properties of single units in optic nerve, superior colliculus, L.G.N. and visual cortex are described in terms of the results of investigations carried out with similar techniques. An extension of Barlow and Levick's directional unit model is presented, based upon optic nerve data. The optic nerve large field off units are described as projecting to the upper part of the stratum griseum superficiale of the superior colliculus where they may function as an 'early warning system'. The considerable differences between the visual cortex organisation of the rabbit and cat is outlined. The universality of the Hubel and Wiesel concept of cortical organisation, which is based upon cat and monkey data, is challenged and the comparative single unit information is examined in detail.

Much space is given to the discussion of comparative retinal unit data. Maturana's concept of deterministic and indeterministic visual systems is considered. The relationship of structure and function in the retina is discussed with respect to various models of unit organisation. Dowling's theory of the seat of visual adaptation is criticised and an alternative offered. The role of the superior colliculus units in the normal animal is discussed but a similar treatment of rabbit visual cortex units is not given because of the inadequacy of the available data.